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THE UNIVERSITY OF ALBERTA

SYSTEMATICS OF THE MOSS CLASS ANDREAEOPSIDA

BY

© BARBARA MITCHELL MURRAY

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

IN
BRYOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
SPRING 1987

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ISBN 0-315-37652-X

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DEGREE: DOCTOR OF PHILOSOPHY IN BRYOLOGY

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Systematics of the moss class Andreaeopsida submitted by Barbara Mitchell Murray in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Botany.

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To

William Campbell Steere

and

William A. Weber

ABSTRACT

The major results of five papers dealing with systematics of Andreaeopsida are: 1) Andreaeopsida consists of two orders: a new order Andreaeobryales B. Murr., based on a single genus and species, *Andreaeobryum macrosporum* Steere & B. Murr.; and Andreaeales, composed of one genus, *Andreaea*, and about fifty species. The newly described beaked mucilage papillae and terete photosynthetic appendages of *Andreaeobryum* are known elsewhere in bryophytes only in *Takakia*, which is proposed to be the closest relative to the Andreaeopsida. 2) *Andreaea sinuosa* B. Murr. a new species from Alaska, British Columbia and Scotland differs from all other ecostate *Andreaeae* by its sinuose cell walls. 3) *Andreaea schofieldiana* B. Murr. and *A. megistospora* B. Murr. ssp. *megistospora* and ssp. *epapillosa* B. Murr. are new costate taxa in sect. *Nerviae* Card. *ex* Broth. from northwestern North America and northwestern Europe. Traditional leaf characters are variable and less reliable than spore size in defining taxa and assessing relationships in sect. *Nerviae*. On the basis of spore size, taxa in sect. *Nerviae* are systematically rearranged. 4) A revision of the Andreaeopsida in arctic North America and Greenland includes eight species and two varieties: *Andreaeobryum macrosporum*, *Andreaea nivalis* Hook., *A. blyttii* Schimp., *A. heinemannii* Hampe & C. Müll. (= *A. blyttii* var. *obtusifolia* (Berggr.) Sharp, *A. angustata* Lindb. *ex* Limpr.; syn. nov.), *A. alpina* Hedw. (new to Greenland), *A. rupestris* Hedw. var. *rupestris*, *A. rupestris* var. *papillosa* (Lindb.) Podp., *A. alpestris* (Thed.) Schimp., and *A. obovata* Thed. (= *A. hartmannii* Thed.). 5) A revision of *Andreaea* in the British Isles includes 11 species, three subspecies, and two varieties: *A. nivalis*, *A. blyttii* (new to region), *A. crassinervia* Bruch (new record), *A. frigida* Hüb., *A. rothii* Web. & Mohr ssp. *rothii* and ssp. *falcata* (Schimp.) Lindb. (= *A. huntii* Limpr.), *A. megistospora* ssp. *megistospora*, *A. alpina*, *A. sinuosa*, *A. mutabilis* Hook. f. & Wils. (new to Northern Hemisphere), *A. rupestris* var. *rupestris*, *A. rupestris* var. *papillosa*, and *A. alpestris*. Material from the British Isles previously identified as *A. crassinervia* and much of the material previously identified as *A. rothii* ssp. *rothii* is redetermined as *A. rothii* ssp. *falcata*.

ACKNOWLEDGEMENTS

In addition to the people and institutions acknowledged in individual chapters, I am indebted to many others.

First I want to thank Dr. Dale H. Vitt, my thesis supervisor, for inviting me to do this study and for his advice and patience. I thank Drs. George E. Ball, David D. Cass, Keith E. Denford, S. Robert Gradstein, and Joseph S. Nelson for their participation as supervisory or examining committee members. I thank the supervisory committee, the Department of Botany, and the Department of Graduate Studies and Research for the flexibility they offered that made this thesis possible.

The University of Alaska Museum, University of Alaska, Fairbanks, provided space, equipment, and resources, including funds for field work, that made the research a pleasure and writing as painless as possible. I especially want to thank Drs. Basil C. Hedrick, Director, and David F. Murray, Curator of the Herbarium, for their support. Expert technical help was provided by: Alan R. Batten, Research Associate, who wrote several computer programs and was always there when questions arose; Barry J. McWayne, Coordinator of Photography; and Sharon A. Olive and Sheila J. Carlson, Administrative Clerks.

All of the line drawings are by Kay W. Holmes, who volunteered a great deal of time to do them. Collaboration with her has been one of the most enjoyable parts of the work.

The personal, professional, and financial support by David Murray for this work is beyond measure, and I am deeply grateful.

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I. INTRODUCTION

This thesis consists of five papers prepared in the course of monographic study of the moss class Andreaeopsida. The most important problems and urgent needs in the systematics of the Andreaeopsida are 1) assessment of the phylogenetic position of the group within bryophytes; 2) analysis of the two included genera: Andreaeobryum, recently described and monotypic (Steere & Murray 1976), and Andreaea, of long standing and comprising about 50 species; and 3) revision of the genus Andreaea.

The first and second problems are the subject of Chapter II. The moss class Andreaeopsida is defined primarily by the occurrence of a valvate capsule. Because valvate capsules occur in liverworts and hornworts but in no other mosses, it has been suggested that the Andreaeopsida represent a link between major bryophyte groups and are perhaps the most primitive mosses extant (e.g. Crosby 1980). Another hypothesis is that the valvate capsule of the Andreaeopsida is derived from a peristomate capsule and the resemblance to capsules of liverworts and hornworts is due to homoplasy (e.g. Robinson & Shaw 1984). Until recently only characters of the genus Andreaea have been available for study. The discovery in 1973 of Andreaeobryum macrosporum Steere & B. Murr. (Steere & Murray 1976) makes it possible to re-evaluate the systematics of the Andreaeopsida taking into account the anomalous features of the new genus. During the present study, additional features were observed in Andreaeobryum, including beaked mucilage papillae, cylindric photosynthetic protonemal appendages, and an apparently unique pattern of perichaetial development. These discoveries led to the proposal in Chapter II that Andreaeobryum and Andreaea represent separate orders and that their closest relative is Takakia, a primitive archegoniate and the only other plant of bryophytic affinity known to have beaked mucilage papillae (Proskauer 1962) and cylindric photosynthetic appendages (Hattori & Mizutani 1958).

Chapters III-VI are revisionary studies of members of the genus Andreaea. Andreaeae occur worldwide in oceanic, temperate and subpolar regions, reaching the tropics only on the highest mountains. Costate species have been revised recently (Schultze-Motel 1970), but the genus as a whole has not been thoroughly monographed. The genus is troublesome because leaf characters that have been used to define taxa tend to vary and are, therefore, difficult to interpret. I have found that these traditional characters are often unreliable. In the present studies new characters, including spore size and cell wall architecture, are used to define taxa and to assess relationships. As a result four new taxa have been described (Chapters III and IV) and members of section Nerviae Card. ex Broth. have been systematically rearranged as compared with the previous revision (Schultze-Motel 1970); see Chapters IV-VI.

The studies presented here concentrate on taxa that occur in the Northern Hemisphere, primarily in North America and Europe. Ample herbarium material was available from these regions, and I was fortunate enough to study most taxa in the field. As background to these regional studies, I have also examined material of Andreaea from throughout the world, including the Southern Hemisphere, where the greatest numerical and systematic diversity occurs. I have used all this material and experience in evaluating and assessing characters and variation and, thus, in reaching the taxonomic conclusions presented here.

Although I have concentrated on two regions, the North American Arctic (Chapter V) and the British Isles (Chapter VI), these two revisions together deal with all the taxa known in North America and Europe and should be of use to workers elsewhere. Keys to ecostate (Chapter III) and costate (Chapter IV) taxa of North America and Europe are provided.

Style and format of Chapters II-VI reflects the requirements of the periodicals in which they have been or will be published.

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Crosby, M. R. 1980. The diversity and relationships of mosses. Pp. 115-129. _In_: R. J. Taylor & A. E. Leviton (eds.), The Mosses of North America. Pacific Division, American Association for the Advancement of Science, San Francisco.

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II. SYSTEMATICS OF THE ANDREAEOPSIDA: TWO ORDERS WITH LINKS TO TAKAKIA[1]

Introduction

Striking differences from and striking similarities to all other major groups of bryophytes have made the valvate mosses, class Andreaeopsida, a systematic perplexity--isolated on the one hand, prototypic and synthetic on the other, both positions implying a long history. Or, to some eyes, the striking features appear derived and homoplastic.

During the past few years of monographic study of the Andreaeopsida I have noticed differences between the two included genera, *Andreaeobryum* and *Andreaea*, beyond those already reported (Steere & Murray 1976). These differences are fundamental and sufficient, in my view, to justify classification of the two genera in separate orders.

Some of the features that separate *Andreaeobryum* from *Andreaea* unite *Andreaeobryum* and *Takakia* and appear to be unknown in other bryophytes. *Takakia* is a genus of uncertain relationships that (like the Andreaeopsida) is considered to possess primitive features, some unique, some moss-like, and some hepatic-like. The phylogenetic relationship of the Andreaeopsida and *Takakia* that is proposed here leads to the assumption of a shared ancestor that has features similar to those proposed by Schuster (1966, 1982, 1984a, b) for a hypothetical bryophyte ancestor. It also supports the views of Schuster (and others) that (at least some) hepatics and mosses have a common ancestry (e.g. Schuster 1984b).

---

[1] A version of this chapter has been accepted for publication. Murray, B. M. Beih. Nova Hedwigia.

The purpose of this paper is to describe and define the Andreaeopsida, to describe and compare the diagnostic features of the two orders, and to assess the relationship of the Andreaeopsida to other bryophytes. Information presented here is based largely on observations of herbarium material, and developmental hypotheses are based on these observations. Unfortunately, I have not studied the German and Swedish languages so cannot do justice to the morphological studies of Andreaea by Berggren (1868) and Kühn (1874). Other than making a few brief translations, I have used distillations by others cited in the text. Likewise, I have cited secondhand the few publications not seen.

For comparative data on other bryophytes, I have relied for the most part on publications. Where original sources are important they are cited, but when information on diagnostic characteristics of various groups is generally available, as in quite a number of recent synoptic and synthetic publications, I have not necessarily cited an authority.

The past ten years or so have seen a resurgence in comparative and phylogenetic study, fostered by numerous papers on single topics (e.g. Hébant 1977, Brown & Lemmon 1984, Filina & Filin 1984), review papers (e.g. A. J. E. Smith 1978, Chopra 1981, Kumar 1984), symposia (e.g. Bryologist 84: 149-215, 1981; J. Bryol. 14: 1-89, 1986), comprehensive volumes (e.g. Suire, ed. 1978; Clarke & Duckett, eds. 1979; Taylor & Leviton, eds. 1980; Schultze-Motel, ed. 1981; Parker, ed. 1982; Schuster, ed. 1983-1984; Dyer & Duckett, eds. 1984; Schofield 1985),

and by application of the cladistic method (e.g. Mishler & Churchill 1984). These works make comparative assessments easier, but since the salient features have been evolving for such a long time in bryophytes and there are only so many morphological possibilities in these relatively simple organisms, it is certainly difficult and in fact may not be possible to determine whether polyphyly or monophyly or analogies or homologies are at hand, or in which direction changes have occurred (Smith 1986). The image provided by Robinson (1985) of phyletic gaps in which divisions could rise and fall is one I enjoy visualizing--in quasi-military terms--and keeping in mind.

Brief History

Members of the Andreaeopsida have been known since the earliest days of bryological study. Dillenius (1741) placed together (in the genus _Lichenastrum_) members of the present-day genus _Andreaea_ and leafy hepatics--an association that was continued by Linnaeus (1753) in the genus _Jungermannia_. Since the Andreaeopsida are the only mosses with longitudinal dehiscence of capsules, the primary mode in liverworts and hornworts, the alliance is understandable. Although Ehrhart (1778) described the new genus _Andreaea_ and recognized its important features, it was Hedwig (1801) who placed _Andreaea_ decisively among mosses, citing possession of a columella, aerial calyptra, and lack of elaters.

Since then views on the genus _Andreaea_ have varied little. Morphological study by Berggren (1868), Kühn (1874), and Waldner (1887, cited by Parihar 1965) have been the foundation for twentieth century phylogenetic speculation and were synthesized and expanded on most recently in general works by Parihar (1965), Watson (1971), and Schofield (1985). The Andreaeopsida have not been completely monographed. Costate species of Andreaea have been treated worldwide (Schultze-Motel 1970), but the most recent works covering the entire genus are out-of-date (Roth 1903-1904, 1910-1911) or synoptic (Brotherus 1924).

Primary systematic features of Andreaea have been thought to be: 1) the valvate capsule, unique among mosses and similar to that of liverworts, 2) the presence of a pseudopodium and dome-like spore sac that overarches the columella, recalling similar features in Sphagnum and hornworts, and 3) protonemal and gametophoric features generally like those of peristomate or so-called true mosses, the Bryopsida, viz. well developed protonemata with multicellular rhizoids, spirally arranged, often costate leaves, etc.

A widely held view is that the Andreaeopsida is an isolated line that has retained many generalized characteristics. Common retention of primitive features in the systematically isolated hepatic lines represented by Haplomitrium and Takakia was discussed by Schuster (1966), who also related Haplomitrium (Calobryales) to Andreaea through the common tendency of the valves to remain attached apically. He further stated "It would seem that the origin of the Bryophytes (with the probable exception of the Anthocerotae) is to be sought somewhere in forms combining the nonderivative characters of the Calobryales, the Andreaeales, the primitive Eubrya (possibly the Tetraphidales), and the fossil Naiaditinae." (Schuster 1966, p. 633).

Ten years ago Steere (in Steere & Murray 1976) described a new family in the Andreaeopsida, the Andreaeobryaceae (based on the monotypic genus, Andreaeobryum Steere & Murray), that differed from the Andreaeaceae primarily in the occurrence of a seta and long tapering bryoid foot, very large spores, a calyptra covering the entire capsule until maturity, and a preference for a limestone substrate. On account of the presence of a seta, it was suggested that the Andreaeobryaceae represented a transitional link between the Andreaeaceae and the Bryopsida.

Systematic isolation of Andreaea has usually been emphasized by class or subclass ranking. Phylogenetic position has always been low on the tree, but branch placement has shifted between other basal groups depending on the weight given various features shared with or lacking in other major groups. Most often Andreaeopsida has been ranked equally with and placed between Sphagnopsida and Bryopsida, or, rarely, within the peristomate mosses, for example by Robinson (1971), who justified this placement by his view that Andreaea was no more different from peristomate mosses than were the Tetraphidaceae which were placed there.

Since the discovery of Andreaeobryum, the Andreaeopsida have been ranked and positioned much as before (Parker 1982, Vitt 1984). Schofield (1980) placed Andreaeobryum in the Andreaeaceae, noting that the differences between Andreaeobryum and Andreaea were insufficient to justify segregation in two families; see also Scagel et al. (1984) and Schofield (1985). Robinson & Shaw (1984) expanded on Robinson's (1971) earlier views stating that similarity of the andreaeopsid and hepatic capsule is due to parallel, purely analogous, development. In their view Sphagnum and the rest of mosses (including valvate mosses) are two systematically isolated groups; both possess an operculum, and an operculum is unlikely to have developed twice, so it is parsimonious to consider the valvate capsule as derived from an operculate one. They suggested the possibility of a relationship between the valvate mosses and the Tetraphidales with its nematodontous peristome with four teeth and thallose protonemal appendages. Filin (1984) reached a similar conclusion based on other data.

Mishler & Churchill (1984), in a cladistic treatment, also considered the andreaeopsid mosses more closely related to the peristomate mosses than to Sphagnum, with the Tetraphidales the most closely related peristomate mosses. In their view, the andreaeopsid and peristomate mosses share the following synapomorphies (lacking in Sphagnum): aerial calyptra, elaborate protonema with elongate cells, elongate antheridia, paraphyses, and costate leaves. The operculum of Sphagnum and peristomate mosses and the pseudopodium of Sphagnum and Andreaea were treated as homoplastic autapomorphies. Mishler & Churchill (1984, 1985) concluded that mosses and tracheophytes are more closely related to each other than either is to liverworts.

Primitive features of the Andreaeopsida have recently been emphasized by its placement by Crosby (1980) and Schofield (1985) at the start of their classifications, and Crosby further stated that he considered Andreaeobryum to possess more of the characters he ascribed to the common ancestor of mosses than any other taxon.

Taxonomy

Class Andreaeopsida

The valvate mosses. Plants perennial, caespitose, poikilohydric, usually on seasonally wet rock, darkly pigmented, green only when young or shaded, lipid-filled. Juvenile stages complex, some persistent or recurring. Protonemata consist of a cell mass that forms within the spore wall; the outer spore coat becomes patchy and dehisces irregularly and from the endosporic cell mass one to several germ tubes emerge; sporelings at this stage frequently seen among perichaetial bracts; when sporelings are attached to normal substrate, cylindric, thallose, persistent, rhizomatic, branched, yellowish protonemata (Fig. II-1: 1, 2), filamentous rhizoids, and thallose appendages are sometimes produced. Secondary protonemata sometimes formed on wounded stem tissue (Fig. II-2: 1, 2). Rhizoids protonemal and basal on stems or innovations, multicellular with oblique crosswalls, uniseriate or in Andreaea also biseriate, red-brown, smooth, often tipped with translucent, presumably cementing material. Stems generally erect, branches irregular, frequently innovative; innovations usually 1-3; stems in transverse section of ± uniform cells, outer cortical cells often smaller and more incrassate than inner, inner cells thin-walled and collenchymatous or with age entire cylinder formed of stereids; central strands absent; brown blobs of unknown provenance (possibly mucilaginous) occasional on stems (Fig. II-1: 9). Axillary mucilage hairs present but dissimilar in the two orders, more numerous and with more numerous stalk cells around sex organs. Leaves polymorphic. Numerous gametophores arise from protonemata (with or without prior formation of protonemal appendages) either as bud-like shoots with leaves becoming gradually larger distally or more often as flagelliform stems with imbricate, minute, scale-like, juvenile leaves that are abruptly differentiated in size and form from mature leaves (Fig. II-1: 7); flagelliform stems also often occur as innovations and areas of juvenile leaves may recur along upper portions of stems. Juvenile leaves minute, up to about 0.4 mm long, usually broader than long, deeply concave, ecostate or weakly costate at zone of transition to mature leaves. Irregularly shaped sometimes filamentous "rudimentary" or primary leaves (Fig. II-1: 6) resembling the pseudoparaphyllia of pleurocarpous mosses present, usually at stem and branch bases. Mature leaves spirally arranged, often brittle, larger and denser on upper portions of stems, sometimes eroded along lower stems; costae occur in both orders; leaves tipped with single cell. Sex organs formed after mature leaves developed. Perichaetia terminal (acrocarpous), bracts differentiated from vegetative leaves; archegonia usually aggregated, at least initially, terminal (acrogynous) or lateral (anacrogynous), red-brown when mature, stalked and often on pedestals (Fig. II-1: 8), neck cells fundamentally 6-seriate; paraphyses very rare. Perigonia terminal, sometimes truely ~~lateral but~~ often only appearing lateral due to renewed stem growth by innovations; bulbiform, sometimes with heads open and like splash-cups when mature, sessile, at least innermost leaves ecostate; antheridia elliptic, 4-10, about 0.2-0.4 mm long, on long stalks with two (rarely more) rows of cells; paraphyses when mature brownish, sometimes with bi- to multi-seriate portions, rarely branched; cells evenly thick-walled, upper cells often short, basal rectangular.

Sporophytes terminal, usually solitary, maturing within gametophytic tissue: a massive epigonium (later calyptra) in Andreaeobryum and a perichaetium in Andreaea. Capsules on short setae in Andreaeobryum, mature sporophytes elevated on pseudopodia in Andreaea; capsules erect, chlorophyllose when young, mostly black when mature, dehiscing by longitudinal valves that do not reach either bases or extreme apices of capsules, valves free distally only when apical tissues disintegrate with age and mechanical stress. Capsule wall multistratose, about 5-10-layered. Epidermal cells of valves with secondary, pigmented, nodular thickenings on radial walls, with thick longitudinal and thin transverse walls; inner cell layers thin-walled, without secondary thickenings, compressed with age; basal epidermal cells with ± evenly thickened walls. Stomata absent. Annuli, opercula and peristomes absent. Sporogenous tissue and columellae presumably derived from the endothecium (reported in Andreaea only); spore sacs dome-shaped, overarching massive, rod-like, persistent columellae that are ± stellate or lobed in transection, spore sacs not separated by air spaces from capsule walls, much spore ornamentation material adheres to tapetum or small globules within spore sac. Spores form, reach mature size and become brown early in capsule development; germination is endosporic and often precocious (occurring prior to dehiscence); spores often remain in tetrads until capsules almost mature but not dispersed in tetrads; spore abortion frequent, often involving a large but variable percentage of the spore mass; very large spores, over 100 µm, occur in both orders (small and medium-sized spores also present in

Andreaea); spores globose, oval, or pyramidal and curvaturate due to mechanical restrictions while in tetrads, often with equatorial ridge, inaperturate, chlorophyllose, usually thick-walled, finely papillose or becoming reticulate-papillose as spore wall stretches during endosporic germination, distal sculpturing higher than proximal. Spores usually mature in spring or summer. Epigonium usually persists until after meiosis, calyptra usually borne on capsule, very rarely remaining partially attached to vaginula.

The class Andreaeopsida has the following features of general occurrence in mosses: 1) extensive heterotrichous protonemata, 2) axillary mucilage hairs, 3) spiral leaf arrangement, 4) costate leaves, 5) paraphyses in gametoecia, 6) a seta (in Andreaeobryum), 7) a columella, 8) a calyptra that is borne on the capsule apex, and 9) spores that are shed gradually.

In addition both genera of the Andreaeopsida share the following features that occur also in some mosses: 1) caespitose habit, 2) darkly pigmented plants filled with cellular lipids, 3) stem lacking central strand, 4) persistent or recurrent juvenile stages, including protonemata, protonemal appendages, and shoots with juvenile leaves, 5) "rudimentary" or primary leaves or filaments, usually at stem or branch bases, 6) archegonia terminal or lateral, with pedestals, 7) perichaetia terminal, 8) elliptic antheridia on long biseriate stalks, formed in bulbiform perigonia, 9) capsule protected to maturity within gametophytic tissue, 10) lack of stomata, operculum and peristome, 11) spore sac overarching massive, persistent columella, not separated from capsule wall by air spaces, 12) much spore ornamentation material lining spore sac and on globs within the spore sac, and 13) frequent spore abortion, often involving a high percentage of the spore mass.

The Andreaeopsida share with the Sphagnopsida the occurrence of a pseudopodium (in Andreaea) and with hornworts and Sphagnopsida a dome-like spore sac. However, in Andreaea the spore sac is of endothecial origin as in peristomate mosses, not amphithecial as in hornworts and Sphagnum.

The major defining features of the class Andreaeopsida are 1) a sporeling with a combination of characteristics that includes development of a cell mass within the spore wall and production of persistent cylindric rhizomatic protonemata, filamentous rhizoids, and erect thallose protonemal appendages, 2) capsules that dehisce by longitudinal slits; and 3) most epidermal cells of the valves with secondary, pigmented, nodular thickenings on the radial walls. As far as I know the cylindric rhizomatic protonemata occur in no other bryophytes; valves with secondary thickenings occur in liverworts and hornworts.

The class Andreaeopsida consists of two monofamilial orders that are represented by two genera Andreaeobryum and Andreaea. Ordinal criteria are presented in Table II-1 and most are illustrated in comparative plates (Fig. II-3-9).

Order Andreaeobryales B. Murray ordo novus

Andreaealibus affinis, a quibus imprimis differt seta, calyptra magna, capsula asymmetrica, valvis irregularibus in sicco involutis sine suturis cellulis epidermalibus parietibus internis tenuibus aliis valde crassis, perichaetio verticillato evoluto post fecundationem cingenti solum archegonium fecundum, papillis mucilaginis rostratis in protonematibus necnon caulibus foliosis, appendicibus cylindricis frequentibus e protonematibus prodientibus. Typus: Andreaeobryaceae.

An order with one family, the Andreaeobryaceae Steere (Steere & Murray 1976), that is characterized by the features of the only known genus and species, Andreaeobryum macrosporum.

Andreaeobryum macrosporum Steere & B. Murr. Fig. II-1-3; 5: 1, 3; 6; 8-15

Phytologia 33: 407. 1976. - Type: Alaska. Brooks Range, Lake Peters, 69°20'N, 145°W; 1974, Murray 6713; holotype in NY, isotypes in ALA and 13 others, seen.

Plants medium-sized to very large and robust, 2-6 or more cm high, black to dark brown, on irrigated calcareous rock and often with whitish calcareous incrustation. Cylindric, unbranched, erect to spreading protonemal appendages, up to about 2 mm long, frequently produced from persistent rhizomatic protonemata or rarely from secondary protonemata on stems. Rhizoids uniseriate, often bearing clavate, terminally beaked or papillose cells, similar to gametophoric mucilage papillae. Secondary protonemata seen frequently on decaying or wounded areas of stems, especially at old stem apices among archegonia. From such redifferentiated embryonic tissue 3-9 fastigiate innovations bearing juvenile leaves may form; alternatively protonemal masses of rhizoids, mucilage papillae and possibly propagative shoot primordia can occur (Fig. II-2: 2, 6). Mucilage papillae variable in position and form, on primary and secondary protonemata and on gametophores at shoot bases, in leaf axils and among sex organs; mucilage papillae elongate, often irregularly curved or strongly bent, gibbous, clavate, with a terminal beak or papilla, open, but apparently plugged with mucilaginous exudate, or closed, lateral walls thin and without breaks; similar to mucilage papillae of Takakia; stalked or very rarely sessile, stalks hyaline to partly brown, one-celled in axillary mucilage papillae, pluricellular around sex organs, rarely branched; in perichaetia mucilage papillae are occasionally borne on multiseriate or partially multiseriate stalks or rarely on apices of tiny perichaetial bracteoles. Mature leaves falcate-secund, narrowly lanceolate, tapering from broad bases to thick, narrowly obtuse subulae, 1.0-1.7 mm long, 0.2-0.25 mm wide near the base. Costae present, single, indistinctly delineated, broad, up to 1/4 or 1/3 the width of leaf bases, filling upper subulae. Laminae ± decurrent, usually unistratose at extreme base, becoming bistratose above. Laminal cells rounded, quadrate to short-rectangular, thick-walled, not pitted, not collenchymatous; 12-14 µm wide, bulging, sometimes with a few low papillae on both surfaces; alar cells not differentiated. Margins plane, entire or crenate below due to bulging cells. Dioicous. Archegonia solitary or up to 10 juxtaposed, often later separated by intercalary stem growth, not formed within a gynoecium. Perichaetial development follows fertilization and a perichaetium surrounds only one fertilized archegonium; unfertilized archegonia are displaced laterally. With fertilization stem growth ceases, "receptacular" tissue enlarges to accommodate deeply penetrating foot and from this expanded embryonic tissue numerous leaf primordia emerge and several closely overlapping gyres of perichaetial bracts form; perichaetial bract insertions are close together, bracts are united to receptacular tissue so that rings of bracts are closely attached basally to stem tissue, some bracts appear connate. Perichaetial bracts variable in size and form: from costate, decurrent with oblate projecting marginal cells, and little differentiated from stem leaves to ecostate and strongly differentiated, large to minute, lobed or entire; minute perichaetial bracteoles bear mucilage papillae apically. Inner perigonial bracts crenate from oblate projecting marginal cells, minute bracteoles sometimes present; paraphyses numerous. Pseudopodia absent.

Sporophytes frequent, single, rarely two sporophytes develop within separate perichaetia if two archegonia are fertilized. Setae and capsules develop ± simultaneously. Setae massive, short and broad, 1.2-1.5(2.0) mm long, 0.2-0.4 mm wide, ridged and flattened when mature, slightly twisted to the left in surface view, cells in surface view rectangular with evenly thickened walls, in longisection central cells thin-walled, end walls transverse to slightly oblique; in transverse section outermost 3-5 rows with round, ± evenly thick-walled cells, innermost 7-11 rows with oval-hexagonal, thin-walled, collenchymatous cells, inner cells hyaline when young, becoming brown, spongy and strongly compressed and collapsed when mature and setae are flattened, with age seta hollow; foot longly tapering as in Bryum, transfer cells well developed, with wall ingrowths; projecting into gametophytic tissue. Capsules to about 1.5 mm long, ± turbinate, elongate-oval when young, becoming broader and tapering gradually to the apex and abruptly to the base, upper valved portion conic with rounded to almost flat apex; capsules little changed in shape by changes in moisture, valves not bulging when mature and dry; capsules often asymmetric, ± oval in transection, due to effect of flattened and slightly twisted seta into which the lower capsule tapers, dehiscence irregular, suture cells absent, valves in conic upper portion of capsule, irregular in number and size, 4-8, often 4-6 main and 1-2 subsidiary valves; valves strongly inrolled when dry, almost flat and slits closed when wet; with mechanical stress and age valves sometimes become free apically or fall leaving a cup-like capsule base. Epidermal cells quadrate to short-rectangular, valves in transverse section with triangular lumens in mature epidermal cells, the inner bases very thin-walled, sides secondarily very thick-walled and pigmented. Outer cells of lower capsule below valves similar to outer seta cells, of 2-3 rows of evenly thick-walled cells (Fig. II-12: 8). Spores very large, spherical to oval, shriveled brown spores about 35-65 μm, turgid green spores about 60-100(122) μm, spore wall thick but fragile, papillose to reticulate-papillose. Spores mature in summer. Sporophyte develops to maturity within epigonium or calyptra; calyptra formed when epigonium ruptures usually near capsule base due to capsule and seta elongation; sometimes capsule pierces epigonium apex or, rarely the epigonium forms a lateral slit through which the capsule is released. Calyptrae large, 0.9-1.5 mm long, multistratose, 4-5-layered, often with scattered large papillae in the middle part (Fig. II-12: 7), covering capsules and, prior to maturity, the upper seta, often persisting to maturity, yellowish brown, mitrate, but often becoming cucullate when capsules widen.

Distribution: Endemic to northwestern North America (Fig. II-10), where Andreaeobryum is sporadic but often locally abundant on wet calcareous cliffs in mountains.

In addition to the features described by Steere & Murray (1976), Andreaeobryum can be differentiated from Andreaea by several others: the terete, frequently produced protonemal appendages (Fig. II-1: 2, 5; 2: 8, 9), the beaked mucilage papillae occurring on protonemata as well as on gametophores (Fig. II-2: 1-8; 3), the position of archegonia and formation of the perichaetium (Fig. II-14; 15: 1), and the structure and dehiscence of the capsule (Fig. II-6; 8). As far as I know these features have not been described in other mosses. The relationship to Takakia, which also has beaked mucilage papillae, is discussed below. Steere & Murray (1976) also mentioned the strikingly large spores. I have since seen spores almost as large in Andreaea megistospora B. Murr. (Chapter IV).

Andreaeales Milde

An order with one family, the Andreaeaceae Dum., that is characterized by the features of its single genus Andreaea. The entire genus Andreaea has not been revised, but I estimate that it comprises fewer than 50 species that can be arranged in several subgenera and sections.

Andreaea Hedw., Sp. Musc. 47. 1801. - Type: A. rupestris Hedw.

Fig. II-4; 5: 2, 4; 7; 9

Acroschisma (Hook. f. & Wils.) Lindley, Veg. Kingd. 63. 1846 (fide Wijk et al. 1959) - *Andreaea* subg. *Acroschisma* Hook. f. & Wils., London J. Bot. 3: 536. 1844. - Type: *A. wilsonii* (Hook. f.) Jaeg.

Neuroloma Card., Rev. Bryol. 38: 50. 1911. *Hom. illeg.*, *non Neuroloma* DC 1824. - Type: *N. fuegianum* Card.

Plants small to large and robust, 0.5-10 or more cm high, brown, purple-red to black, on acidic to mildly basic rock or lithosols. Sparse, small, dorsiventral protonemal appendages rarely seen. Rhizoids uni- and bi-seriate, lacking clavate, terminally beaked cells. Secondary stem protonemata infrequent. Mucilage hairs axillary only, stalked, similar to those in many mosses, with 1-3(4, rarely more) quadrate, brown stalk cells and 1(2-more in inflorescences) elongate, cylindric or clavate mucilaginous cell that is hyaline or brown with age, outer wall thin and often with breaks along surface or appearing collared, mucilage presumably secreted through wall and ruptured cuticle. Mucilage hairs in perigonia sometimes transitional in form to paraphyses. Mature leaves variable in orientation and shape: in ecostate taxa often falcate-secund, usually clasping below, ± spreading above, and ± constricted, like a waist, near mid-leaf and apices incurved or secund; in costate taxa ± abruptly contracted to the subulae and often secund above; usually somewhat narrowed to a straight insertion, rarely auriculate. Costae, when present, variable in form in different taxa: single or branched, distinctly or indistinctly delineated, short to excurrent, broad or narrow, strong throughout or lacking apically or basally; in transverse section of ± uniform, thick-walled cells. Submarginal costa-like bands present in one species. Laminal cells variable: in ecostate species usually short above, becoming rectangular to elongate below mid-leaf and basal marginal cells ± differentiated; in costate species often short throughout, some subcostal cells rectangular; laminal cells usually unistratose in ecostate species, usually bi- to multi-stratose, at least locally in costate species; transverse walls very thin, longitudinal walls often thick and pitted, rarely thin or unpitted, sometimes smooth or sinuose. Margins usually plane to somewhat incurved, reflexed in a few species. Asexual reproduction from gemma-like branching filaments produced from laminal cells seen in only one species. Usually cladautoicous, often difficult to demonstrate due to brittle stems; rarely dioicous or gonioautoicous. Archegonia aggregated, about 3-6, rarely solitary, formed within a gynoecium, rarely secondarily laterally displaced. Perichaetial bracts large, usually 4-6, often differentiated, convolute and sheathing, inner bracts often tattered distally. Innermost perigonial bracts sometimes with crenate margins, toothed in one species; paraphyses few or numerous. Sporophytes exserted when mature on a pseudopodium that lengthens quickly mostly by cell elongation. Pseudopodia slender, green when young becoming pale brown to black, slightly twisted to the left in surface view, in transverse section consisting of stereids, often persisting after decay of sporophyte; pseudopodia usually naked, in a few species bearing unfertilized archegonia and sometimes rudimentary leaves and mucilage hairs well up the stalk.

Sporophytes known for most species and usually present, usually single, rarely double and bipseudopodiate. Setae undeveloped, sporophyte consists of capsule and bulbous to shortly tapering foot with moderately developed transfer cells. Capsules about 0.5 to 2.0 mm long, when dry contracted and valves bulging, when wet elliptic and valves closed; capsule ± symmetric, dehiscence by 4 or rarely 6-10 valves; capsule apex conic-apiculate; margins of valves ± reflexed when dry, plane to slightly incurved when wet; bases from (1/8)1/4-1/2(over 3/4) the length of the capsules. Epidermal cells rectangular to long-rectangular, with pore-like thinnings at transverse wall area, sutures of thin-walled cells that form lines of dehiscence present; valve epidermal cells usually oval and with all walls thick in transverse section, all inner walls secondarily darkly pigmented, outer walls tan. Cells of lower capsule similar to valve cells but lack secondary thickenings. Spore abortion frequent or in several species rare; spores small to very large, (10)13-60(110) µm, spore wall sometimes fragile, usually papillose to reticulate-papillose, rarely almost smooth. Spores mature from spring to fall. Calyptrae very small, consisting chiefly of unmodified archegonial necks, (1)2(3)-layered, delicate and membranous below neck, campanulate-mitrate, persistent or not.

Distribution: Generally distributed in subpolar and oceanic mountainous regions of both hemispheres; in tropical areas only on the highest mountains.

The major diagnostic features of _Andreaea_ are outlined in Table II-1. As can be seen also by comparing Fig. II-3-9, _Andreaea_ and _Andreaeobryum_ are very different, and no intermediates are known. It is clear from the sharp morphological and developmental differences that the two lines have been isolated for a very long time.

Comparative Features of Andreaeobryum and Andreaea

Juvenile Stages

Juvenile stages occur between spore germination and sexual maturity, and it is in these stages that the majority of systematic features that define the Andreaeopsida are found. In addition to their valvate capsule the Andreaeopsida are characterized primarily by complex and persistent protonemata, which may also recur on mature plants. Conditions that control development are not known, but a fundamental plasticity is evidenced by the production of different structures from the same type of primordial cell, e.g. protonemal appendages or gametophores, juvenile or mature leaves, and, in *Andreaeobryum*, mucilage papillae or rhizoids. Both genera have similar patterns of spore germination, spore abortion, protonemal development, and gametophores with juvenile leaves. The major differences are the occurrence of protonemal mucilage papillae and the regular formation of cylindric protonemal appendages in *Andreaeobryum*. Both features seem to be unique for mosses and are similar to organs in *Takakia*.

Spore germination and early sporeling development

Observations of *Andreaea* have been made primarily by Berggren (1868), Kühn (1874), Nehira (1963, 1976, 1983), and Nishida (1971, 1978). My observations largely corroborate theirs, and Andreaeobryum follows a similar pattern. Spores of the Andreaopsida form and mature early in the development of the capsule. In most species spore abortion occurs (Fig. II-11: 1; 12: 9) and can involve a large but variable portion of the spore mass. Spores become multicellular within the spore wall, often prior to capsule dehiscence. The globose to ovate cell masses formed have two to many cells, and spore size in the group reflects this endosporic increase in volume due to cell division. In any one species the size range of living spores is large, the largest spores often about twice the size of the smallest (e.g. in Andreaea blyttii Schimp. from 10-23 µm, in A. megistospora B. Murr. and Andreaeobryum from about 50-110 µm). As the spore wall stretches to accommodate the growing cell mass, the papillose ornamentation becomes reticulate and patchy (Fig. II-11: 1, 2; 12: 9, 10). The spore wall is thick, but, especially in species with the largest spores, it can be very fragile (the pressure of a coverslip is often enough to break open the exospore and release the contents as a green amorphous mass). After capsule dehiscence one to several germ tubes emerge, and the spore coat breaks open irregularly. The germ tubes are uni- or bi-seriate filaments or multiseriate cylinders and consist of rhizoids, caulonemata, chloronemata, and in A. macrosporum also protonemal mucilage papillae. Sporelings at this stage (Fig. II-12: 11) are often seen within perichaetia or among leaves. In culture, Nishida (1978) saw leafy gametophores produced directly from the globose endosporic cell mass, but I have seen this only once in herbarium material.

The germination pattern of the Andreaeopsida no doubt provides a sporeling, at the time of capsule dehiscence, that is prepared for immediate growth should conditions be favorable or possibly for a resting stage. An ability to shut off development after initial sporeling formation until conditions are appropriate for further growth is postulated, but experimental work has not been undertaken. Endosporic germination is generally considered an adaptation to xeric conditions, at least seasonally, and is usually found in what are considered specialized mosses, but it could well be a very early adaptation of plants emerging into a xeric habitat--land.

The Andreaeopsida have a wide range of spore size, about 10-110 um in Andreaea and 50-125 um in Andreaeobryum. Medium-sized spores are often considered plesiomorphic for bryophytes, but large spore size could have enhanced the survival of a precociously germinating spore, since a much larger protective cell mass can be formed within the spore coat. Determining the direction of evolution of this character in the Andreaeopsida may not be possible. Large spores are often found in imperfectly dehiscing capsules in specialized groups which suggests that the feature is not primitive. On the other hand, fossils of early land plants with possible bryophytic affinity include large-spored taxa with unclear means of dehiscence, e.g. Horneophyton and Naiadita. And Bhutta (1973, cited by Taylor 1982) reported multicellular gametophytes in spores of Horneophyton.

Sporeling establishment and protonemal development

When sporelings are attached to the normal substrate, persistent, rhizomatic, branched, cylindric, yellowish protonemata form that have many rhizoidal branches (Fig. II-1: 1, 2). Numerous gametophores can ultimately be produced from one protonemal mat. In Andreaeobryum rhizoids are almost always completely uniseriate, in Andreaea uniseriate and biseriate. Walls are usually smooth; rarely have I seen peg-like thickenings on inner surfaces (cf. Redhead 1973).

The protonemal mat grows on the surface of and also penetrates the outer layer of the rock substrate. The mechanism of penetration is unknown, but there is presumably a mucilaginous material that permits tight attachment to the substrate (Redhead 1973).

As far as I know, cylindric persistent rhizomatic protonemata are not known in other bryophytes, nor are biseriate rhizoids in mosses. Longitudinally and transversely septate, digitiform rhizoidal apices occur in hepatics in Schistochilaceae (Schuster & Engel 1977, 1985). In many mosses protonemata are ephemeral and consist of uniseriate filaments. Perennial protonemata occur in some groups, such as the Ephemeraceae, whose gametophores are short-lived, and the Grimmiaceae, which grow in similar habitats to those of the Andreaeopsida.

The production, in Andreaeobryum, of similar, clavate, beaked mucilaginous cells on both protonemata, including rhizoids, and gametophores, in leaf axils and among sex organs (Fig. II-2: 1-8; 3), is unique. It seems clear that the two structures, rhizoids and mucilage papillae, have the same derivation. Axillary and gametoecial mucilage papillae (discussed below) were probably derived from the protonemal form, and they elaborated stalks and leaf-like bases as their function became protection of embryonic tissues. It does not seem likely that the mucilage papillae of Andreaeobryum are modified from other types of filaments or from leaves. Schuster (1967) suggested that in hepatics leaves could evolve from mucilage papillae. The elaborate stalks and perichaetial bracteoles bearing mucilage papillae in Andreaeobryum (Fig. II-2: 3, 4) show how this could occur in mosses.

Protonemal mucilage papillae are unknown in other mosses; beaked mucilage papillae are known only in the genus Takakia. The relationship between Andreaeobryum and Takakia is discussed below.

Andreaeobryum and Andreaea can both form thallose, chlorophyllose protonemal appendages; conditions necessary for formation are unknown. Protonemal appendages are rare in herbarium material of Andreaea, but scarcity may be, in part, due to lack of observation, since most material is gathered without the substrate attached. In Andreaeobryum, however, they are frequent, terete and up to about 2 mm long (Fig. II-1: 3-5), differing in form from the small, dorsiventral appendages of Andreaea (figured by Berggren 1868, Kühn 1874). Protonemal appendages of Andreaea resemble the pseudoparaphyllia-like primary leaves that occur most often at the bases of innovations in the Andreaeopsida (Fig. II-1: 6), and it may be that these structures are homologous.

Andreaeobryum material that was kept over winter in subarctic conditions in Alaska produced numerous chlorophyllose appendages as soon as snow cover melted. Such rapidly produced, low-growing outgrowths or enations are no doubt energetically efficient photosynthetic organs.

Thallose protonemata are rare in mosses and are found in groups of uncertain phylogenetic position but which are often considered to retain primitive features (Sphagnopsida, Tetraphidaceae, Diphysciaceae, in addition to the Andreaeopsida). In the Andreaeopsida, gametophores can form in the absence of protonemal appendages. Schofield (1981, 1985) said that in other mosses, protonemal appendages precede gametophores. Protonemal appendages have been considered to be derived and to correlate with specialized epilithic habitats (Schofield 1981, Crandall-Stotler 1984), but there is no clear evidence of this. Crandall-Stotler (1984) noted that the major similarity in sporeling development in mosses, hepatics, and hornworts is endosporic germination and the occurrence of prothallial forms in non-mesic habitats and that such patterns are parallel adaptations to similar habitats. Crandall-Stotler (1980) and Mishler & Churchill (1984) also considered the complex protonemata of the Andreaeopsida to be derived or modified from filamentous forms. I see no reason why precocious endosporic germination, complex thallose protonemata and protonemal appendages could not, in some cases, represent very early specializations of land plants especially since they occur in groups generally held, on other grounds as well, to be the most primitive representatives of bryophytes. Similar reasoning has been presented by Robinson & Shaw (1984) to highlight relationships between valvate mosses and the Tetraphidaceae.

Thus, the plastic protonemata of the Andreaeopsida with their varied special structures serving as perennating organs, hold-fasts, and clone-producing rhizomes and with the ability to produce protective mucilaginous hairs and rhizoids and, under appropriate environmental conditions, low-growing photosynthetic appendages, could be a model for an effective early land plant. Features such as these, possibly in existence before erect leafy axes were developed, could have enabled the plant to withstand water stress and large amounts of UV radiation, and may represent retained primitive traits. These adaptations and others permit some members of the Andreaeopsida today to inhabit the most stressful environments of all in terms of moisture, temperature, and exposure.

Another possibility, suggested by the fundamental differences in the protonemata of the Andreaeopsida from those of other mosses, is that andreaeopsid rhizoids and rhizomatic protonemata are uniquely derived and not related to the rhizoids and filamentous protonemata of other mosses.

Formation of the gametophore and its juvenile stages

A bryophyte gametophore is formed when a lateral initial on the protonema differentiates an apical cell and typical three-dimensional growth ensues (Knoop 1984). It is not known what conditions (environmental, internal, or a combination) control whether an apical initial is formed laterally on the cylindric protonema of the Andreaeopsida. Sometimes the initial fails to form and a photosynthetic protonemal appendage is produced instead of a stem axis (Kühn 1874). Under appropriate conditions, however, a faceted apical cell is produced and gametophores form. In the Andreaeopsida two juvenile forms of leaves occur, primary leaves and juvenile leaves, which may precede the production of typical mature leaves.

Primary leaves: At the extreme bases of stems and branches, often within gynoecia, are frequently seen irregular filamentous or leaf-like structures. These structures are also seen occasionally along stems where there is no apparent branch primordium (Fig. II-1: 6). Similar structures have been termed variously: primary leaves, accessory leaves, rudimentary leaves, paraphyllia, and pseudoparaphyllia. See Ireland (1971) and Buck (1984) for comparative terminology and discussions of paraphyllia and pseudoparaphyllia, structures in mosses considered confined to pleurocarpous mosses. Primary leaves of the Andreaeopsida are irregular in occurrence, shape, and size. They can be filamentous, partly filamentous and partly multiseriate or leaf-like and uni- or partly pluri-stratose. They are minute or up to 1 mm or so long. These leaves, which occur in both Andreaeobryum and Andreaea, are similar in form, and are perhaps homologous, to the dorsiventral protonemal appendages of Andreaea. They also recall the pseudoparaphyllia of pleurocarpous mosses in both form and position.

Juvenile leaves: Buds of gametophores can develop immediately into shoots bearing mature leaves, but much more commonly the leaves along a greater or lesser extent of basal stems and branches differ strongly in size and shape from ordinary leaves. These leaves are usually termed juvenile leaves or scale-leaves (Fig. II-1: 7; 13: 1, 9), and they range from minute to larger structures that intergrade into the typical mature leaves.

The juvenile leaves of the Andreaeopsida and the other specialized leaves formed by the group (gametoecial, primary) are simpler in form than the mature leaves. They have few cell types and are generally ecostate, even in costate taxa, except in the zone of transition to mature leaves. Whether these simpler forms are primitive or derived is not determinable. It may be that they are simply different, and serve a different function under differing environmental conditions as has been suggested for other mosses (e.g. Zander & Hoe 1979, Mishler 1986).

It is likely that the abrupt leaf dimorphism is a response to change in environmental conditions (light, moisture, temperature etc.). Juvenile leaves occur commonly in several groups of mosses, especially those in epilithic habitats (Pottiaceae and Grimmiaceae, for example) and have been considered specializations. But as with other features so considered (precociously germinating spores, protonemal appendages) they may be manifestations of early adaptations to land where simple, low-growing, opportunistic photosynthetic structures could be advantageous. The occurrence of juvenile leaves in many bryophytes, including groups that appear to have retained primitive features, Haplomitrium, Takakia, Tetraphidaceae, and Polytrichaceae, among others, could be a result of their occurrence early in bryophyte evolution, just as they may be later specializations in some other bryophytes. There are two ways to look at such features: as modifications for dry habitats in various primitive mesic forms, therefore developed in parallel by many groups, or as modifications to the early dry habitat, land, therefore early derived features common to certain lines of land plants. Both views have merit.

Asexual Reproduction

In the Andreaeopsida, numerous gametophores can be produced from one protonemal mat. Following growth and branching, clones are formed by decay of older stems. Stems and branches usually have an initial period of growth by proliferation of imbricate juvenile leaves that precedes the production of mature leaves and sex organs; in fact, flagelliform shoots with juvenile leaves may proliferate at branching points; whorls of up to nine shoots may be produced as innovations, but more commonly one to three are formed.

Regeneration, whereby gametophytic cells redifferentiate, become embryonic, and produce new gametophytic plants, is considered to be a primitive evolutionary character in land plants (Bopp 1983). In *Andreaeobryum* secondary protonemata form frequently on stems, usually where tissues are damaged or decaying, often at old apices among archegonia. From this regenerative tissue large mats of mucilage hairs and often rhizoids form (Fig. II-2: 1, 2). Such rhizoid-mucilage hair mats can be precursors to bud or protonemal appendage formation. Sometimes numerous propagula are seen on these pads of mucilage papillae and rhizoids. These are easily detached and consist of short stems with, apparently, positively geotropic rhizoids and negatively geotropic mucilage hairs and minute leafy buds (Fig. II-2: 6). Whether these minute plants become detached and form independent gametophores in nature is unknown.

I have seen gemma-like structures on leaves in only one species of *Andreaea*. In *A. urophylla* Robins., for which sporophytes are unknown, numerous, short or long, branching filaments are produced from bulging leaf cells. The filaments, or gemmae, can develop into multiseriate, cylindric branched protonemata, become detached, and produce rhizoids and leafy buds (Murray unpublished data). What triggers the production of the filaments and whether it can be induced in other species with bulging laminal cells is unknown. As with the production of secondary protonemal masses on stems, it seems to occur most often in old, decaying leaves.

Mature Gametophore

Stem

No developmental study has been made of conducting tissue in *Andreaeobryum*. As in *Andreaea* (Hébant 1977), the central stem tissue seems to consist of pitted conducting parenchyma, and no distinct central strand is apparent (Fig. II-13: 6). Young stems often have thin-walled and pitted central cells, but in old stems all cells are often stereids.

Leaves

The production of mature leaves, usually followed by sex organs, marks the mature gametophore. As discussed above, juvenile and protonemal structures may recur on mature plants, most notably on innovations, which have basal rhizoids and primary leaves and frequently several millimeters of juvenile leaf growth. Mature leaves are more elaborate in form and cell types than are primary or juvenile leaves. No specialized conducting tissue is present in costate species (Fig. II-13: 4, 5). Kühn (1874) discussed similarities in cell division during leaf development between *Andreaea* and hepatics, on one hand, and mosses such as *Sphagnum* and *Tetraphis*, on the other. Crandall-Stotler (1984) pointed out that the leaf development, reported by Kühn (1874), from a dome-shaped, rather than a two-sided, apical cell in *Andreaea* was an exception to the normal bryophytic pattern. Emig (1921 reviewing Pottier 1920) reported that, in *Andreaea angustata*

Lindb., the single sided apical cell may be replaced by an initial with two faces and that leaves formed from an initial cell with two faces are ecostate and those from a one-sided initial cell are costate. Whether such a switch is involved in heterophylly in the Andreaeopsida is unknown.

Mucilage papillae

The mucilage papillae of Andreaea are always hair-like (stalked) and axillary. Stalk cells are brown and quadrate to short-rectangular, and the mucilaginous cells, which may be several, are cylindric to clavate, hyaline or brown with age, and persistent or evanescent (Fig. II-4). The mucilaginous cells are thin-walled with numerous breaks in the outer cuticle that sometimes give a collared appearance (as in Diphyscium). Mucilage formation has not been demonstrated in the Andreaeopsida but it appears to be the same as in other mosses (Wanstall 1950).

Mucilage papillae in Andreaeobryum differ in position and form from any reported for mosses, including Andreaea. The mucilage papillae of gametophores are one-celled, broadened above to gibbous, irregularly curved to strongly bent, mottled brown, thin-walled, with a terminal beak or papilla through which mucilage is apparently extruded. They can be sessile or, much more commonly, stalked. Mucilage papillae are frequent around archegonia where stalks are from one to several cells high, irregularly multiseriate, or mucilage papillae can occur rarely on the tiny bracteoles adjacent to developing sporophytes (Fig. II-2: 1-8; 3; 14: 1, 2).

Mucilage papillae in *Andreaeobryum* are very similar to those in *Takakia*, and in no way resemble those of *Andreaea*, which are typically moss-like. Given a protonemal origin for mucilage papillae in *Andreaeobryum* and no evidence of protonemal mucilage papillae in *Andreaea*, it is possible that axillary hairs in *Andreaea* have a different origin and that the two structures are not homologous. If derivation is similar, strong evolutionary divergence has occurred.

Just as there are no morphological links between the mucilage hairs of *Andreaeobryum* and those of *Andreaea* and other mosses, Schuster (1984a) suggested that the mucilage papillae of *Takakia* are not homologous with those of other hepatics and that slime papillae have probably originated several times to meet specific needs, not only the primary need of lubricating shoot apices. The positions of the gametophoric mucilage hairs in *Andreaeobryum* are like those in hepatics rather than in mosses, where they occur only in leaf axils. In hepatics, such as *Frullania* (Schuster 1966), they occur on diverse parts of the plant, between archegonia, at apices of immature leaves, or underleaves may be reduced to slime papillae. In hepatics, as in *Andreaeobryum*, slime papillae are often in part transformed into pluricellular structures with multiseriate bases.

Position of sex organs

The Andreaeopsida are dioicous or more commonly cladautoicous, that is with each sex on a separate axis. Crandall-Stotler (1984, Pl. I: 6) figured an inflorescence of *Andreaea rothii* Web. & Mohr termed synoicous, but, unfortunately, the antheridia are not clear in the published photograph.

In cladautoicous species, branch systems often bear a single sex for a considerable period of time, which leads to the separation of the sexes and a decreased possibility of inbreeding; however, presumably when environmental conditions permit, a unisexual branch system can suddenly produce organs of the other sex. For this reason it is difficult to conclude that a species is obligately dioicous, and few seem to be. This pattern of sex organ distribution that usually promotes outcrossing but can permit inbreeding in leafy liverworts is discussed by Longton & Schuster (1983, p. 446): "We have here a fascinating model: one spore, carrying both ♂ and ♀ chromosomes, giving rise to a genetically bisexual gametophyte which 'separates' gynoecia and androecia temporarily to the point where inbreeding becomes difficult, if not impossible. Yet, if no opportunity for outbreeding occurs, one can visualize a situation where a 'late' archegonium is fertilized by sperms from an unduly 'early' antheridium and vice versa."

Archegonial position is also flexible. The Andreaeopsida are acrocarpous; perichaetia are always terminal, and after fertilization further growth is from innovations within perichaetia. Old sporophytes (like perigonia) can appear lateral due to subsequent innovative growth. Although archegonia are usually formed in terminal groups, with subsequent growth by innovative branching (acrogynous), they can also be remote and lateral--more commonly in Andreaeobryum than in Andreaea. In some instances it appears that the lateral position is because the apical cell is not spent in the production of archegonia and further stem growth takes place; this pattern is termed anacrogynous. In other instances, the lateral position may result from displacement of terminal, aggregated archegonia by intercalary stem growth. Anacrogyny is difficult to determine by study of herbarium material. Usually innovations can be detected by the presence of basal rhizoids and a slight narrowing of girth and change in direction of growth. In the absence of these clues, one can hypothesize that main stem growth is continuing and archegonial formation is anacrogynous. Lateral archegonia are very rare in acrocarpous mosses, and it is not known if the lateral position is the result of continued stem growth or of displacement from a terminal head by growth of intermediate tissues (Chopra & Sheel 1974). A combination of acrogyny and anacrogyny, including lateral displacement, such as occurs in the Andreaeopsida, is present in Haplomitrium subg. Haplomitrium (Engel 1981, 1982).

In Andreaea, as is typical of mosses, archegonia are produced in a gynoecium of small, often sheathing or tubular leaves. The cluster of about three to six archegonia remains within the developing perichaetium. Unfertilized archegonia only rarely become secondarily lateral and are seen among the outer perichaetial bracts. Usually they remain at the base of or, in some species, scattered along the pseudopodium.

In Andreaeobryum archegonial position differs. From one to about ten archegonia can be formed in close proximity, but each one is protected by mucilage hairs and often surrounded by leaf primordia and young leaves. Unlike Andreaea, the fertilized archegonium is solitary within the perichaetium which develops after production of archegonia, mostly after fertilization. Unfertilized archegonia that may have been aggregated when produced become scattered among leaves on the stem below the sporophyte or one or two may remain among the outermost perichaetial bracts.

Antheridia are clustered in bulbiform perigonia that are usually terminal or sometimes truely lateral. Numerous perigonia can be formed in close proximity on branches or branch systems; they look like beads on a string. I do not know if several generations can form in a single season, but the often greater number of antheridial, as compared with archegonial, generations on adjacent branches suggests that they can.

Protection of the sporophyte

In the Andreaeopsida, sporophytes develop to maturity within the protection of gametophytic structures. Such protected development occurs in a few mosses, Sphagnum and Archidium, for example, but it contrasts sharply with development in most mosses in which the capsule matures after seta elongation. Schuster (1979) stated that no group of land plants other than hepatics has wholly internalized the sporophyte until maturity, thus removing it from normal selection pressures. He hypothesized that internalization occurred at the very start of hepatic evolution which explains the relative uniformity of the hepatic capsule and the gametophytic diversity. The internalization of sporophytic development in the Andreaeopsida (and the Sphagnopsida) suggests that the feature may be plesiomorphous for bryophytes.

Perichaetium: As stated above, aggregated archegonia form within gynoecia in Andreaea, but not in Andreaeobryum. Perichaetial formation in Andreaea proceeds as in other mosses; after fertilization, gynoecial leaves develop into large protective perichaetial bracts. In most species the bracts are sheathing and tubular, and the sporophyte develops to maturity within their protection.

In Andreaeobryum perichaetial development contrasts sharply with that in Andreaea--and, as far as I know, in other mosses. After archegonia form, numerous leaf primordia appear among archegonia and mucilage hairs as emergences in varying stages of development and without obvious phyllotaxy (Fig. II-14: 1, 3). Prior to fertilization, stem growth can separate archegonia along the leafy stem. After fertilization, the stem into which the foot will penetrate thickens, and a widened region of receptacular tissue forms; mucilage papillae and leaf primordia emerge from irregular bulges (Fig. II-14: 4, 5). Internodal growth ceases, and numerous bracts of variable shape and degrees of development surround the young capsule in several tightly compressed gyres. Thirty or more bracts can make up the perichaetium. Bracts are extremely diverse in size and form (Fig. II-14: 6, 7); some are quite similar to mature vegetative leaves, others are ecostate and variable in shape, from linear to lanceolate or reniform. The innermost are tiny and can bear mucilage papillae. Some are lobed and appear fused basally. This may be a result of intimate connection of individual bracts with each other and with stem tissue. Bracts remain attached to stem tissue when one attempts to scrape them from the stem (Fig. II-14: 2).

Calyptra: In most mosses the epigonium (the archegonial envelope that protects the developing sporophyte) ruptures very early, prior to meiosis and capsule development, and forms a calyptra that is borne on the apex of the sporophyte. In hepatics the archegonial envelope (when developed) protects the sporophyte until maturity and is usually ruptured at the extreme apex. In the Andreaeopsida (and in the Sphagnopsida), the epigonium ruptures and the calyptra is formed when capsule development is well underway and after meiosis.

Mishler & Churchill (1984) interpreted calyptral development in the Andreaeaopsida to be like that of most mosses and unlike that of Sphagnum, hepatics, and hornworts. However, even though the andreaeopsid epigonium does not tear at the extreme apex as in hepatics and Sphagnum, development is otherwise very like that of Sphagnum and seems nearer that of hepatics than that of other mosses.

In Andreaea the epigonium becomes fragile and membranous as capsule elongation occurs. The rupture occurs above the middle of the capsule and the apical remnant, or calyptra, is often seen on the elevated capsule apex, the most conspicuous part being the unmodified archegonial neck (Fig. II-5: 2; 7: 1). In Andreaeobryum the epigonium enlarges early and is massive and multistratose. It often encloses the developing sporophyte until it is nearly mature. As the capsule and seta elongate, the epigonium tears at the upper seta, and the calyptra formed often remains on the capsule until it is mature. The archegonial neck disintegrates early but the lower part is long-lasting (Fig. II-5: 1; 6: 1; 15: 1-4). When young the calyptra has large papillae on its middle part (Fig. II-12: 7; 14: 4).

Pseudopodium: The capsule in Andreaea is protected by the perichaetium until spores are ready for dispersion, at which time modified stem and archegonial tissues undergo rapid cell elongation to form a pseudopodium. In several species, mostly in subgenus *Chasmocalyx* (Braithw.) Lindb., the pseudopodium retains what is probably a more primitive, stem-like character. Reduced leaves, axillary hairs, and unfertilized archegonia can be scattered along it. In most other *Andreaea* species, the stalk is naked.

In *Andreaea* the mature capsule breaks through the usually tubular perichaetial sheath as it is pushed up by the elongation of the pseudopodium. It is of interest that all *Andreaea* capsules have an apiculate apex, whereas the *Andreaeobryum* capsule, protected in a massive calyptra and with a crown-like rather than a tubular perichaetium, has a more or less flattened or obtuse apex. Most hepatic capsules have rounded apices, but some groups with marsupia have beaks. Schuster (1984a) has suggested an analogy to the egg-tooth of an emerging chick, whereby the evolving beak is linked with the reduction and loss of the calyptra and the evolution of a thick wall that the escaping capsule must push through.

In *Andreaeobryum* stem elongation stops abruptly with the onset of capsule development; in some species of *Andreaea* (in subgenus *Chasmocalyx*), the upper leafy stem elongates considerably during capsule development, and in all *Andreaea* species the gametophytic stalk, the pseudopodium, elongates by intercalary growth after the capsule is mature.

Pseudopodia occur in the genus *Sphagnum* and have been reported elsewhere in mosses only in the genus *Neckeropsis* (Touw 1962). In *Sphagnum* unfertilized archegonia occur at the capsule base above the foot; in *Andreaea* they occur at the base of or on the surface of the pseudopodium. The pseudopodium of Andreaea is undoubtedly independently derived from those of other mosses.

Sporophyte

Foot

As Crandall-Stotler (1984) has pointed out, when a seta meristem is absent, only a bulbous or small conic foot will be formed. Thus the differences in shape of the foot of Andreaea (bulbous to short conic) and Andreaeobryum (dagger-shaped) can be related to differences in growth, a seta meristem never being produced in Andreaea. In both genera transfer cells are developed, strongly so in Andreaeobryum (Fig. II-12: 6).

Seta

Seta and capsule develop simultaneously in Andreaeobryum, unlike most mosses where the seta develops prior to the capsule and prior to meiosis. In Andreaeobryum the seta is massive and short. No central strand is present, but there is a distinct large central cylinder of cells with extremely thin walls except in corners, where strong collenchymatous development occurs. These cells are hyaline when young but become extremely spongy and are collapsed and rust-colored when mature. Mature setae are strongly flattened and often hollow due to the collapse of the delicate inner cylinder (Fig. II-6:4; 12: 1-4). In longisection the cells of the cylinder are similar to the outer cortical cells, oblong with slightly oblique cross-walls, however they have thinner walls and become rust-colored and devoid of contents.

Mishler & Churchill (1984) considered setae in mosses and liverworts independently derived. It seems likely to me that the presence of a seta is plesiomorphic in bryophytes. Seta development in Andreaeobryum seems to have more in common with that of primitive liverworts, which have massive setae with thin-walled cells (Schuster 1966), than that of other mosses. It is possible that the massive seta of Andreaeobryum, with the inner cylinder collapsing with age, is primitive and that the ephemeral aerial axis elevating mature capsules of hepatics evolved from a similar structure. Setae of hepatics prior to rapid final cell elongation often are similar in length to that of Andreaeobryum.

Capsule

Just as the formation and structure of the capsule stalk is completely different in Andreaeobryum and Andreaea, so is the structure and dehiscence of the capsule. The main differentiating features are outlined in Table II-1 and illustrated in Fig. II-5: 3, 4; 6-9. I can see no relationship between the two capsules beyond the facts that secondary pigmented thickenings are present and dehiscence is along longitudinal lines, features lacking in other mosses but present in many hepatics and hornworts. The secondary thickenings in the two genera, which no doubt strengthen the capsule wall and regulate dehiscence, are laid down differently (compare Fig. II-8 & 9). There does not even appear to be a basic four-parted symmetry, evident in

Andreaea, in the capsule of Andreaeobryum (compare Fig. II-6 & 7). The capsule of Andreaeobryum is somewhat dorsiventral and asymmetric, due to the flattening and twisting of the massive seta. The upper seta and lower capsule cortical cells are similar to each other (Fig. II-12: 1, 8). Because there are no regular lines of dehiscence with specialized suture cells such as occur in Andreaea and in hepatics, the valves in Andreaeobryum are formed very irregularly along lines of least resistance in the irregularly arranged, secondarily thickened epidermal ~~cells~~ (Fig. II-6: 5, 6; 8: 5). Four or five, rarely six, irregular main valves are formed, often with several smaller subvalves that do not reach the apical tissue (Fig. II-6: 3, 5, 6; 15: 5). The valves are strongly inrolled when dry and almost plane when wet; repeated wetting and drying causes stress to the tissue and over a period of time the apical or basal valve tissue breaks leaving either teeth-like processes (Fig. II-15: 6) or a cup-like base (Fig. II-15: 7). In Andreaea, by contrast, the capsule is usually symmetric and with four (rarely more) valves (Fig. II-7). Valve placement is always determined by lines of specialized thin-walled suture cells (Fig. II-5: 4; 9: 1-3), similar to those in many hepatics. Valve margins are slightly reflexed when dry and almost plane when wet.

In neither genus is there a trace of an operculum. Apical capsule cells are differentiated from valve cells (as are basal cells), but there are no specialized separating cells. I see no reason to assume that the operculum developed but once in bryophyte evolution or that the andreaeopsid capsule is derived from an operculate one, as postulated by Robinson & Shaw (1984). The structure is simple and the occurrence of operculate (as well as inoperculate) dehiscence in ascomycetes and hepatics (Marchantiales) illustrates that it can be a homoplastic feature.

Because there are no intermediate forms between the two types of capsules and no similar structures in other bryophytes, I do not think it possible to determine the direction of evolutionary change of characters involved in capsule dehiscence. The occurrence of suture cells (that serve the same function as the annulus in operculate mosses) in *Andreaea* and in many hepatics suggests that this feature is plesiomorphous; but irregular dehiscence, sometimes appearing longitudinal, is present in some early land plants (e.g. *Sporogonites* [Halle 1916]) so this may be a primitive form and suture cells may be homoplasies in *Andreaea*, liverworts, and hornworts.

Ultrastructure

Spermatogenesis

Duckett et al. (1983) reported results of spermatogenesis studies that showed that spline apertures are two tubules wide in *Andreaea*, *Tetraphis*, and *Sphagnum* and one wide in most other moss genera. Spline widths did not prove to be very useful taxonomically, but the widest splines are 57 tubules in the hepatic *Haplomitrium* (Carothers & Duckett 1979) and 44 tubules in the moss *Timmiella* (Gambardella & Sposito 1982, cited by Carothers & Brown 1985). Spline widths in tubules for most hepatics are from 13-23, for most mosses 12-15. *Andreaea rothii* is one of few exceptions with 23 tubules (Carothers & Duckett 1978). Nothing is known about spermatogenesis in *Andreaeobryum*.

Duckett & Carothers (1979) reported that in most moss antheridia, jacket cells are uniformly thin-walled but that Andreaea appears to be unique since the antheridia have three longitudinal grooves from tips to bases of the gamete cavity and the jacket cells subtending these grooves are smaller and thicker walled than the other cells.

Spore wall formation

Recently two studies of spore wall formation in Andreaea have been made (Brown & Lemmon 1984, Filina & Filin 1984). Brown & Lemmon (1984) studied A. rothii and concluded that development in Andreaea differs from that of other vascular and nonvascular cryptogams in that no trilaminar elements are present, that is no inner lamellate layer is involved in the formation of exine. They considered (p. 412) that "this ultrastructural evidence of departure from the fundamental pattern of exine development in mosses supports the taxonomic isolation of Andreaea from mosses of the Sphagnopsida and Bryopsida." Filina & Filin (1984), in their study of spore wall development and structure in A. rupestris, also found no lamellae. However, they felt that the conclusion that tripartite lamellae always participate in the formation of exine in mosses is premature since lamellae have been found in just a few mosses.

Brown & Lemmon (1984) reported that the exine is first initiated as discrete, irregular globules within the sporocyte wall and later loosely compacted to form an incomplete layer. Since the paper by Filina & Filin is not readily accessible and their interpretation of spore wall development differs from that of Brown & Lemmon, I have translated several passages (p. 89): "There appears by the end of cytokinesis, on the distal surface of protoplasts of young spores, a wavy layer, in section appearing interrupted, composed mostly of electron-dense homogeneous plates, in all probability of substances that are precursors of sporopollenin. This wavy layer represents the rudiment of the future acetolysis-stable membrane layer. It is possible that the material for its construction came partially from the protoplasts of the spores, since the dark layer does not closely abut the plasmalemma, instead between them lighter sections with bubbles are visible.. With growth of the spores the electron dense plates merge together forming a more or less uninterrupted layer....The special wall undergoes a very great reorganization: in it, especially in the zone bordering the spores appear numerous osmiophilic globules gradually accumulating on the surfaces of the plates...."

Filina & Filin (1984) compared their findings of _A. rupestris_ with literature reports and microphotographs of other mosses and concluded that there is (p. 96) "no doubt that the initial stages in the formation of the spore wall in many bryoid mosses proceeds in the same way as in _A. rupestris_, that is osmiophilic globules, which appear in the special wall of the sporocyte and the intersporal partitions, participate in its construction.. Evidently in most mosses thus far studied homogeneous exine results from the merging of osmiophilic globules and the remarkable transformation of their substances. In other words, the way the homogeneous exine of mosses is formed is not different, in our view, from the acetolysis-stable lax layer of the sporoderm of _A. rupestris_."

In partial contradiction to the conclusion reached by Brown & Lemmon (1984), Filina & Filin (1984) felt that in spore wall ultrastructure the Andreaeaceae are similar to many bryalean mosses and remarkably distinct from Sphagnum.

Filina & Filin noted the presence of an acetolysis-unstable outer layer which they considered to be comparable to the pollenkitt of anemophilous angiosperm pollen grains. This layer may be the same as the electron dense material that occludes interstitial regions in A. rothii as described by Brown & Lemmon (1984).

Nothing is known of spore wall development in Andreaeobryum.

Cytology

Nothing is known about Andreaeobryum and little work has been done on Andreaea. The chromosome number n=10 is reported for six species of Andreaea: A. australis F. Muell. ex Mitt. (Newton 1980), A. depressinervis Card., A. gainii Card. (Kuta et al. 1982), A. nivalis Hook. (Yano 1961, 1962, cited by Fritsch 1982), A. rothii (Anderson & Bryan 1958), and A. rupestris (Khanna 1964). Smith & Newton (1968) reported n=11 for Welsh material of A. rothii. I have examined the cytological vouchers of A. rothii. Eastern North American material treated by Anderson & Bryan is A. rothii ssp. rothii. The Welsh material is A. rothii ssp. falcata (Schimp.) Lindb.

Chemistry

Nothing is known of *Andreaeobryum* and little of *Andreaea*. In the recent review of bryophyte chemistry, *Andreaea* is included only in a table listing steroids (Huneck 1983). Flavonoids have not been found in *Andreaea* (McClure & Miller 1967, cited by Huneck 1983).

Suire & Asakawa (1979) felt that the complete acetylation of D-methionine by *Andreaea* and *Sphagnum* supported their separation as classes from other mosses. However, Filin (1984) reported that Pokorny (1974), to whom Suire & Asakawa referred, reported similar methionine metabolism also in the genus *Bryum*. Mishler & Churchill (1984, 1985) considered the ability to distinguish D-methionine from L-methionine a synapomorphy separating hornworts, mosses and tracheophytes from liverworts.

Relationship between *Andreaeobryum* and *Takakia*

Brief history of *Takakia*

Since its discovery in 1951 (Hattori & Inoue 1958), *Takakia* has been considered by most hepaticologists a very primitive archegoniate representing "an isolated branch [that] originated among the ancestors of modern bryophytes" (Hattori & Mizutani 1958, p. 302). It is most closely related to *Haplomitrium* among hepatics but also has affinities to mosses. Literature on *Takakia* has been summarized up to 1968 by Hattori et al. (1968) and from 1968 to 1973 by Hattori et al. (1973). Crandall-Stotler (1986) listed most recent references, to which can be added other systematically useful papers, Hattori et al. (1974) and D. K. Smith (1978).

Takakia has been variously classified because of its possession of features that are hepatic-like, moss-like or unique. Because critical structures such as antheridia and sporophytes are unknown and many of its features are considered primitive its placement remains controversial. Most often it has been treated as a liverwort in an order near the Calobryales (Hattori & Inoue 1958) or in a suborder within the Calobryales (Schuster 1967). Mizutani (1972, cited by Hattori et al. 1974) erected a new class within mosses to accommodate Takakia, and Crandall-Stotler (1986) segregated it in a new division.

The genus Takakia consists of two species found only in the Northern Hemisphere, T. ceratophylla (Mitt.) Grolle (Sikkim, eastern Nepal, Alaska) and T. lepidozioides Hattori & Inoue (northern Borneo, eastern Nepal, Japan, Alaska, British Columbia); see maps in Hattori et al. 1974, Smith 1978.

Among the hepatic-like features of Takakia are the pitted water conducting cells, found elsewhere only in Haplomitrium and Metzgeriales (Hébant 1973, 1979); anacrogynous archegonia (Hattori & Mizutani 1958), and a basically hepatic-like chemistry, although hopane-type triterpenes considered characteristic of some mosses also occur (Asakawa et al. 1979).

Several characteristics of Takakia are shared with Haplomitrium alone among hepatics: leafless rhizomatic axes, axillary and rhizomatic mucilage papillae, much mucilage secretion, and lack of rhizoids, (cf. Hattori et al. 1974). The occasional broken apical slime cap of mucilage papillae in Haplomitrium hookeri (Sm.) Nees was compared to the open beaked mucilage papillae of Takakia by Worley (1969). Membrane-enclosed oil bodies, found in most liverworts including Haplomitrium, are lacking in Takakia (Hattori et al. 1974).

Moss-like features of Takakia include axillary mucilage papillae and archegonia that are chlorophyllose (Hattori et al. 1968), have six rows of neck cells (Inoue 1961, cited by Hattori et al. 1968; Hattori et al. 1968) and sit on pedestals (Mizutani 1967, cited by Hattori et al. 1968; Hattori et al. 1968).

Several features have been considered peculiar to Takakia among bryophytes. These include: beaked mucilage papillae with mucilage exuded from burst beaks, occurring on both rhizomatic and leafy axes and differing from the axillary mucilage papillae that lack beaks (Proskauer 1962), cylindric leaves, and irregular phyllotaxy (Hattori & Mizutani 1958). Another unusual, primitive feature in Takakia similar to that in hornworts, Isoëtes and Selaginella and one whose systematic significance is unknown, is the occurrence of only one or two plastids in meristematic stem apex and leaf primordium cells (Proskauer 1962, Fig. 11, Crandall-Stotler 1986, Fig. 33). Chromosome numbers of n=4 and n=5 reported for Takakia (Tatuno 1958, Inoue 1973) are not known in hepatics.

Students of Takakia have commented on its unusual growth that shows a plasticity that does not appear to be genetically fixed. Such growth has been considered primitive. Hattori & Mizutani (1958) reported new shoots forming from epidermal cells or cell masses on stems as well as by regeneration from meristems on detached leaves. Hattori et al. (1968) reported that rhizome growth was meristematic but that leafy stems were formed when an apical cell with three cutting faces was produced. They also described the ability of each type of axis to produce branches of the other type. Proskauer (1962) also reported this type of meristematic growth and wondered at the role of the apical cell in such a system. Chopra (1981) suggested that typical three-dimensional bryophytic growth was not yet genetically fixed, since subterranean axes always had meristematic apical growth and leafy shoots could grow either with or without an apical cell. Crandall-Stotler (1986) undertook an ultrastructural study to determine the growth system in Takakia. She confirmed that rhizomatic growth in Takakia is meristematic, from a dome of meristematic cells; she found a similar growth pattern in leafy shoots and that each cylindric leaf developed independently from a single epidermal initial (Crandall-Stotler 1986, Fig. 28). This growth pattern differs from that of Haplomitrium in which both rhizomes and leafy shoots grow by means of segmented apical cells (Leitgeb 1875, cited by Crandall-Stotler 1986). The smooth rhizome apices of Takakia that contrast with those of Haplomitrium, which are mammillose from bulging epidermal cells and mucilage papillae, are mentioned by Hattori & Mizutani 1958 and figured by Crandall-Stotler (1986, Fig. 21, 22). Crandall-Stotler concluded that the lack of apical cell growth and the presence of generalized meristematic growth differentiates Takakia "from all other extant bryophytes" (1986, p. 19).

Comparative Features

Three of the major features of Andreaeobryum that distinguish it from Andreaea (see Table II-1) are apparently also unknown in the

Sphagnopsida and the Bryopsida. These are the cylindric form of the protonemal appendages (the closest known are the funnel-shaped appendage of the Diphysciaceae and the spatulate one of the Tetraphidaceae), the beaked mucilage papillae, and the development and structure of the perichaetium. The natural development of secondary protonemata and numerous branch buds especially on decapitated stems is another striking feature of Andreaeobryum. Since beaked mucilage papillae have been reported previously only in the genus Takakia, a comparison of morphological characteristics of the two genera was made.

Mucilage papillae

The mucilage papillae of Andreaeobryum and Takakia are morphologically similar. Mucilage papillae of Andreaeobryum are illustrated in Fig. II-2: 2-8; 3; 14: 1 and can be compared with illustrations of those in Takakia by Hattori & Mizutani (1958, Fig. 1: k, s [as a fungus]; 2: c, d [as fungi], h), Proskauer (1962, Fig. 2-10), Hattori et al. (1968, Fig. I: 16; II: 8; III: 28,), and D. K. Smith (1978, Fig. 3: i-n; 4). In addition to structural similarity, mucilage hairs in the two genera occur in similar positions on both rhizomatic and leafy axes. Mucilage papillae are often massed and are often seen at the bases of outgrowths or enations. Compare Fig. II-2: 8 with Fig. 1: s of Hattori & Mizutani (1958). On erect axes mucilage papillae in both genera occur in leaf axils, among sex organs, and at the bases of outgrowths or enations. In Andreaeobryum they occur at the bases of regenerative shoot primordia (Fig. II-2: 6); similar structures are known in T. ceratophylla (D. K. Smith 1978, Fig. 4).

Rhizoids are present in Andreaeobryum but are absent in Takakia. As stated above mucilage papillae and rhizoids appear to have the same derivation in Andreaeobryum. These observations together with the morphological and positional similarity of mucilage papillae in Andreaeobryum and Takakia, support the hypothesis of Hattori et al. (1974) that mucilage pads on lower shoots in Takakia are possibly homologous with rhizoids in Musci though differing in function. Schuster (1977), expressed a similar view, concerning hepatics, that rhizoids and mucilage papillae are very similar ontogenetically and that perhaps mucilage papillae are derived from a pre-existing holdfast in primitive gametophytes and thus may derive from rhizoids arrested in early developmental stages. Whether Takakia ever had the ability to produce true rhizoids is unknown.

Proskauer (1962) discussed the possibility that the open, beaked mucilage papillae of Takakia might attract a mycorrhizal partner. But, as he stated, the presence of hyphae inside papillae is not conclusive. In Andreaeobryum fungal hyphae have been seen around the beaks. However mucilage papillae originated, it seems clear that the main function is protection of embryonic tissue in both genera.

On account of similarity in structure, similarity in position, and apparent similarity in function, I propose that the mucilage papilla of Andreaeobryum and Takakia is a uniquely shared homologous feature that defines a clade including the Andreaeopsida and Takakia. Whether this is a retained primitive feature lost in related bryophytes or a uniquely derived feature is not determinable.

Cylindric photosynthetic appendages

The protonemal appendages of Andreaeobryum and the so-called leaves, phyllids, or enations of Takakia could be unrelated, yet they are similar in structure and unknown in other bryophytes. Compare Fig. II-1: 3-5; 2: 8, 9 of Andreaeobryum with numerous illustrations of Takakia in Hattori & Mizutani (1958), Hattori et al. (1968, 1973), D. K. Smith (1978), and Schuster (1984b). Both structures are produced without a faceted apical cell. In Andreaeobryum they are produced from cylindric protonemata of the rhizomatic axis (Fig. II-1: 2 shows the abrupt change from one to the other) or from secondary protonemata on stems; in Takakia they define the so-called leafy axis. The cylindric enations in both genera appear more shoot-like than leaf-like. Schuster (1984b) reported that shoot-like leaves of Takakia sometimes develop archegonia from their apices and suggested (p. 901) that "the anomalous structures in Takakia, sometimes called leaves, may have evolved wholly independently from 'leaves' in other bryophytes...."

The remote common ancestor of Takakia and Andreaeobryum could, like the hypothetical hepatic ancestor of Schuster (1979), have lacked true leaves and rhizoids. Instead it may have had total meristematic growth or incomplete fixation of apical cell growth, simple enations such as mucilage papillae and cylindric photosynthetic emergences, and prostrate and possibly also differentiated aerial axes. Subsequent evolution could have led to further differentiation of the two axes and development of apical cell growth and true leaves in the Andreaeopsida. Although the structure and development of the rhizomatic protonema in Andreaeobryum and the rhizomatic axis in Takakia are undoubtedly different, both patterns could have evolved from a radially symmetric axis growing by a generalized meristem in a remote common ancestor. Such a rootless, leafless prostrate axis has been suggested by many as the ancestor for archegoniates.

The cylindric photosynthetic enations may represent leaf-precursors in Andreaeobryum, where the costate leaves could have evolved from the costa-like protonemal appendages by planation and lamina development for more efficient photosynthesis. It is possible that leaves in the Andreaeopsida are not homologous to leaves in other mosses.

The juvenile protonemal phase of Andreaeobryum may retain many of the characteristics of the ancestral plant: a cylindric rhizomatic axis with meristematic growth and with the ability to produce mucilage papillae, perhaps first as holdfasts, and to send forth erect photosynthetic enations when conditions were appropriate.

Structure, position and protection of archegonia

The archegonia of Andreaeobryum and Takakia both have pedestals and necks are composed of six cell rows. The latter characteristic is common to mosses, but archegonia with pedestals have been reported, as far as I know, only in Splachnobryum and Splachnum (Chopra & Sheel 1977). Archegonia in Andreaeobryum and Takakia are anacrogynous and solitary, features that also occur in some other bryophytes. The unusual perichaetium described above for Andreaeobryum appears to be unique among mosses. Unfortunately, male plants and sporophytes are unknown in Takakia, so perichaetial development is unknown, however, archegonia seem to be similarly surrounded by mucilage papillae and numerous irregularly developing leaves in both genera. Compare Fig. II-14: 1, 3 of Andreaeobryum with Fig. 3: j of Takakia in Hattori & Mizutani (1958). In both genera leaf arrangement becomes dense, internodes shorten drastically, and leaf primordia occur irregularly; in Andreaeobryum spiral arrangement is lost, and the role of the apical cell in leaf production is unclear.

Cytology

Since nothing is known about the cytology of Andreaeobryum, it can only be said that the number n=10 of Andreaea is non-controversial as far as a relationship with Takakia goes.

Distribution

Whether the primarily Northern Hemisphere distribution of Andreaeobryum and Takakia could result from Laurasian origin is not determinable. It is interesting that several primitive groups of mosses may well have originated there, Sphagnopsida, Tetraphidales, Buxbaumiales for example (Schuster 1983).

Conclusions

The traditional view of the Andreaeopsida, which this study endorses, is that the group is primitive, not only cladistically but patristically. That is, the ancestors of the group are ancient, and the group has retained many primitive features. Assessing phylogenetic relationships is difficult, if not impossible, because of the morphological discontinuities between the two orders and also between the Andreaeopsida and possible outgroups. It must also be kept in mind that one of the sister groups, the Andreaeobryales, is represented by a single species, Andreaeobryum macrosporum, and that the taxon with which it shares several features, Takakia, consists of only two species in which male plants and sporophytes have never been found. Since there are no conclusive reports of fossil Andreaeopsida from earlier than the Pleistocene and all are referable to extant taxa (Miller 1980, 1984), this record is not helpful in assessing phylogenetic relationships.

Several possibilities (or combinations of these possibilities) exist, among which are: 1) that the Andreaeopsida is not related to other bryophytes but arose independently, 2) that it has a common ancestry only with other mosses, 3) that it shares ancestry with Takakia and through Takakia possibly with hepatics such as Haplomitrium, 4) that the Andreaeopsida and Takakia link hepatics and mosses, and 5) that the Andreaeopsida and Takakia clade has hepatic-like and moss-like features that were derived independently.

The third and perhaps the fourth possibilities seem most reasonable to me, and in this paper I have tried to substantiate this view. I have presented information that supports the view that the Andreaeopsida is a monophyletic group of mosses defined by unique sporeling features and mode of capsule dehiscence, and I consider it a class distinct from the Sphagnopsida and the Bryopsida. It may well be that mosses represent a grade but not a clade. The features that the Andreaeopsida share with the Bryopsida are chiefly gametophytic, and it is possible that divergence or evolution of the two lines occurred prior to the evolution of leaves and some protonemal features. Much evidence has accumulated showing that hornworts and Sphagnopsida are very isolated groups, and the Andreaeopsida do not appear to have significant affinity with either group.

The Andreaeobryales and Andreaeales are sharply differentiated from each other on several criteria (Table II-1). Assessment of evolutionary trends, or polarity, of these features requires that a third taxon cladistically more primitive than the sister groups, Andreaeobryales and Andreaeales be examined. Usually (Robinson & Shaw 1984 and Mishler & Churchill 1984, for example) characteristics of other moss groups have been used to evaluate those of the Andreaeopsida, in other words mosses have been considered cladistically primitive to the Andreaeopsida. This assumption would lead to the conclusion that unique features of Andreaeobryum, such as beaked mucilage papillae, cylindric protonemal appendages, and the perichaetium, are derived compared to their counterparts in Andreaea, which are similar to features found in other mosses. If mosses are the outgroup, then the similarities between Andreaeobryum and Takakia would be seen either as homoplasies or Takakia would have to be considered as derived within the Andreaeopsida clade.

If, on the other hand, Takakia is considered the outgroup of the Andreaeopsida, Andreaeobryum is a primitive taxon without clear autapomorphies. Its distinctive features are synapomorphies of the Andreaeopsida--Takakiopsida clade, and the diagnostic features of

Andreaea are autapomorphies. Indeed, retention of primitive features in *Andreaeobryum* and *Takakia* makes *Andreaeobryum* seem more remote in some ways from *Andreaea* than from *Takakia*. Extinctions and divergence are also reponsible for the sharp morphological discontinuities between the Andreaeobryales and Andreaeales.

The morphological links between *Andreaeobryum* and *Takakia* have led me to consider the Andreaeopsida most closely related to the Takakiopsida by virtue of shared unique features discussed above. That the Takakiopsida is the outgroup of the Andreaeopsida seems to me to be the most feasible choice based on the structural evidence.

Although there is controversy as to the degree of relationship between *Haplomitrium* and *Takakia*, there is sufficient evidence of closeness to support the view that the two genera share remote ancestry, viz. similar rhizomatic shoots lacking rhizoids, hepatic-like conducting tissue found elsewhere only in some thalloid Metzgeriales, anacrogynous archegonia that do not form within gynoecia, and similar mucilage papillae. Additionally, *Takakia* has a hepatic-like chemistry albeit quite divergent from that of *Haplomitrium* (Asakawa et al. 1979). Since the relationship of *Takakia* and *Haplomitrium* cannot be clarified without knowledge of sporophytes in *Takakia*, it is practical to treat *Takakia* and *Haplomitrium* at the same rank as the Andreaeopsida and as representing the classes, Takakiopsida and Haplomitriopsida. If the Haplomitriopsida are related to the Takakiopsida probably other hepatics are too, since it is likely that diagnostic features for hepatics, elaters, oil bodies, and lunularic acid, present in *Haplomitrium*, arose but once.

The recent study by Crandall-Stotler (1986) is of great interest. She presented further evidence of the distance of Takakia from other archegoniates in its meristematic growth pattern. It seems to me that the widely held view that the class Takakiopsida represents the most primitive bryophyte known is valid and that Takakiopsida is cladistically related to the Andreaeopsida and most probably to the Haplomitriopsida as well. Obviously the patristic distance between the Andreaeopsida and the Haplomitriopsida is very great.

Whether, or at what level, other mosses can be included in this lineage cannot be determined by the present study. It seems significant that the Andreaeopsida and hepatics lack stomates, so if the Andreaeopsida are related to other mosses, a very remote stomatose ancestor from which the andreaeopsid-takakiopsid ancestor was derived is one possibility. The fossil record is not helpful and the time is so remote that it is impossible to do more than speculate. Intriguing similarities between the Tetraphidales and the Andreaeopsida, mentioned above, and chemical and morphological similarities between the Andreaeopsida and other mosses make the possibility of a cladistic link attractive.

If my assessment is valid, the ancestor of the Andreaeopsida and the Takakiopsida probably had radially symmetric, prostrate and erect axes; formed beaked mucilage papillae on both axes; produced cylindric, shoot-like photosynthetic enations and possibly scale-like enations; grew meristematically and possibly also by a single apical initial, which may not have been genetically fixed; was dioicous; had lateral archegonia with six rows of neck cells and pedestals; and lacked gynoecia. It seems likely that rhizoids and specialized conducting tissue were present if one considers the fossil record of early land plants.

If the Haplomitriopsida are accepted in the clade, further hypotheses concerning the ancestor are possible. It had aggregated antheridia with long stalks, sporophytes that matured within protective gametophytic tissue, a massive, short seta, a cylindric capsule lacking stomates and opening by apically coherent longitudinal valves, and spores that divided within the spore wall and produced massive protonemata. Since both Haplomitrium and Andreaea have suture cells, it is possible that this feature is plesiomorphous. Again, although the fossil record is too incomplete to permit detailed analysis, the occurrence in early land plants of columellae and overarching spore sacs (Horneophyton, Sporogonites), multistratose capsule walls, as well as other features already postulated adds to the picture of a possible ancestor (Stewart 1983). Ancestral reconstructions for bryophytes along these general lines have been suggested by others (Schuster 1979, Crosby 1980 for example). Whether there was a single archegoniate ancestor or multiple ancestors with similar features is part of the mystery.

Further study can fill many gaps in the knowledge of plants with valvate, estomatose capsules. Even if sporophytes of Takakia cannot be found or induced (Hattori 1980), much remains to be learned about Andreaeobryum, its morphogenetic patterns, ultrastructure, cytology and chemistry, for example, that should show if the above assessment can be upheld. And perhaps in fossils of early land plants structures similar to the beaked mucilage papillae can be found. In the meantime the

Andreaeopsida remain an important piece in the puzzle about land plant origins.

Acknowledgements

I am very grateful to D. H. Vitt and D. F. Murray for discussion and criticism; to Kay W. Holmes for the line drawings; to G. Braybrook and C. LaFarge-England for help in preparing the SEMs at the Department of Entomology, University of Alberta, Edmonton; to J. J. Engel for information and criticism; to the curators and staffs of many herbaria for loans; and to C. Batten for numerous collections of excellent material of Andreaeobryum. Writings of R. M. Schuster were a major stimulus for this paper.

Table II-1. Diagnostic differences between Andreaeobryales and Andreaeales.

	Andreaeobryales	Andreaeales
Protonemal appendages	frequent, terete, up to 2 mm long (Pl. 1: 3-5; 2: 8, 9)	rare, dorsiventral, up to 0.4 mm long
Mucilage papillae	on protonemata and gametophores; sessile, stalked or on bracteoles; stalk cells hyaline to partly brown, rectangular; mucilage papillae weakly to strongly curved, gibbous, with apical beak; mucilage secretion apparently apical (Pl. 2: 1-8; 3)	in leaf axils only, stalked; stalk cells brown, quadrate; mucilage papillae straight, cylindric or clavate, lacking apical beak; mucilage secretion apparently through breaks in lateral walls (Pl. 4)
Perichaetium	developed after fertilization, enclosing fertilized archegonium only; of compacted gyres of numerous, variable leaves (Pl. 6: 2; 14)	developed in part prior to fertilization, enclosing aggregated archegonia; of several concave or convolute leaves (Pl. 7: 2)
Capsule elevation	during maturation on short, stout seta, pseudopodium absent (Pl. 5: 1)	after maturity on pseudopodium, seta undeveloped (Pl. 5: 2)
Capsule shape	little changed wet or dry, turbinate, obtuse-conic, ± asymmetric (Pl. 6; 15: 4-5)	contracted and valves bulging when dry, lengthened, elliptic and valves plane when wet, apiculate, radially symmetric (Pl. 7)
Dehiscence	irregular, sutures of thin-walled cells absent (Pl. 8: 5)	± regular, along sutures of thin-walled cells (Pl. 5: 4; 9: 1-3)
Valve arrangement	irregular, often 4-5 main and 1-2 shorter valves; valves inrolled when dry (Pl. 6)	usually regular, valves 4(6-10), slightly reflexed to plane when dry (Pl. 7)
Valve epidermal cells	quadrate to short-rectangular, in transection triangular, inner walls very thin, other walls with pigmented secondary thickenings (Pl. 5: 3; 8)	long-rectangular, in transection ± oval, all walls thick, inner and radial walls with pigmented secondary thickenings (Pl. 5: 4; 9)
Calyptra	large, multistratose, covering entire capsule, (Pl. 5: 1; 6: 1)	small, mostly bistratose, apical, (Pl. 5: 2; 7: 1)
Substrate	calcareous rock	acidic or mildly basic rock or soil

Figure II-1. Illustrations of Andreaeobryum macrosporum. -- 1. Cylindric rhizomatic protonemata and rhizoids. -- 2. Cylindric protonemata (left) and cylindric protonemal appendage (a). -- 3. Protonemal mat with erect protonemal appendages (left) and bud of gametophore (right). -- 4. Protonemal appendages, some broken showing transections. -- 5. Transection of protonemal appendage. -- 6. Primary leaves on stem. -- 7. Apex of shoot bearing juvenile leaves. 8. Archegonium with basal pedestal. -- 9. Brown blob of unknown provenance on stem. 1, 2, 5, 6 & 9 bar scale = 25 µm; 3, 4 & 7, bar scale = 250 µm. (Alaska, ALA. 1 & 2, Light Microscope [LM]: Murray 6482; 3-5, SEM: Murray 8753; 6 & 7, SEM and 8 & 9, LM: Batten 75-43.)

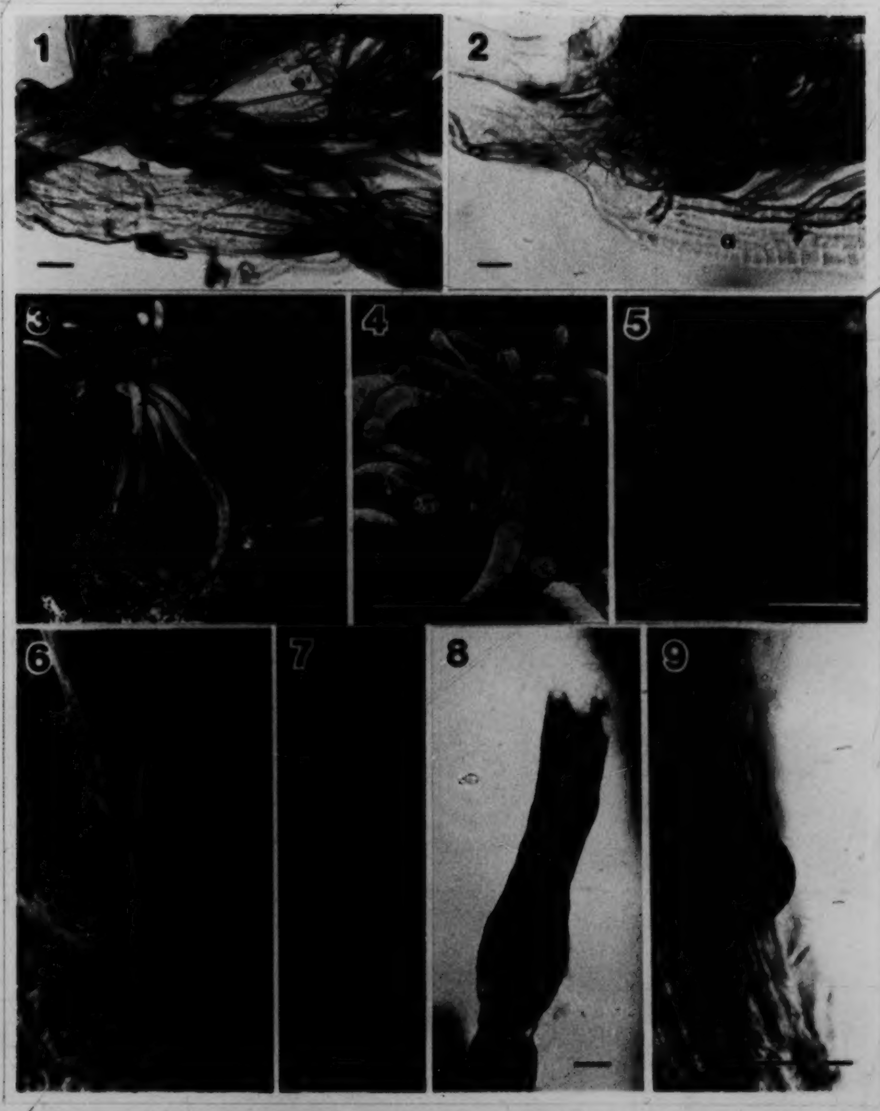
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Figure II-2. Protonemata and mucilage papillae in *Andreaeobryum macrosporum*. -- 1. Protonemal appendages and bud of gametophore from decaying stem. -- 2. Secondary protonemata of rhizoids and mucilage papillae from wounded stem apex. -- 3. Perichaetial bracteole with apical mucilage papilla -- 4 & 5. Perichaetial mucilage papillae, 4, with multiseriate stalks, 5, with uniseriate stalks. -- 6. Propagula-like bud from secondary protonemata, with basal rhizoids (positively geotropic) and mucilage papillae (apparently negatively geotropic). -- 7. Clavate mucilage papillae on rhizoids. -- 8. Mucilage papillae surrounding protonemal appendage, most with one stalk cell, one branched. -- 9. Transections of protonemal appendages. (Alaska, ALA. 1, 4 [right], 5 [bottom]: *Batten* *75-43*; 2: *Batten* *75-41*; 3, 5 [upper right] & 6: *Murray* *5068*; 4 [right], 3 Aug. 1986, *Murray* *&* *Perry* *s.n.*; 5 [upper left], 7-9: *Murray* *8753*.)

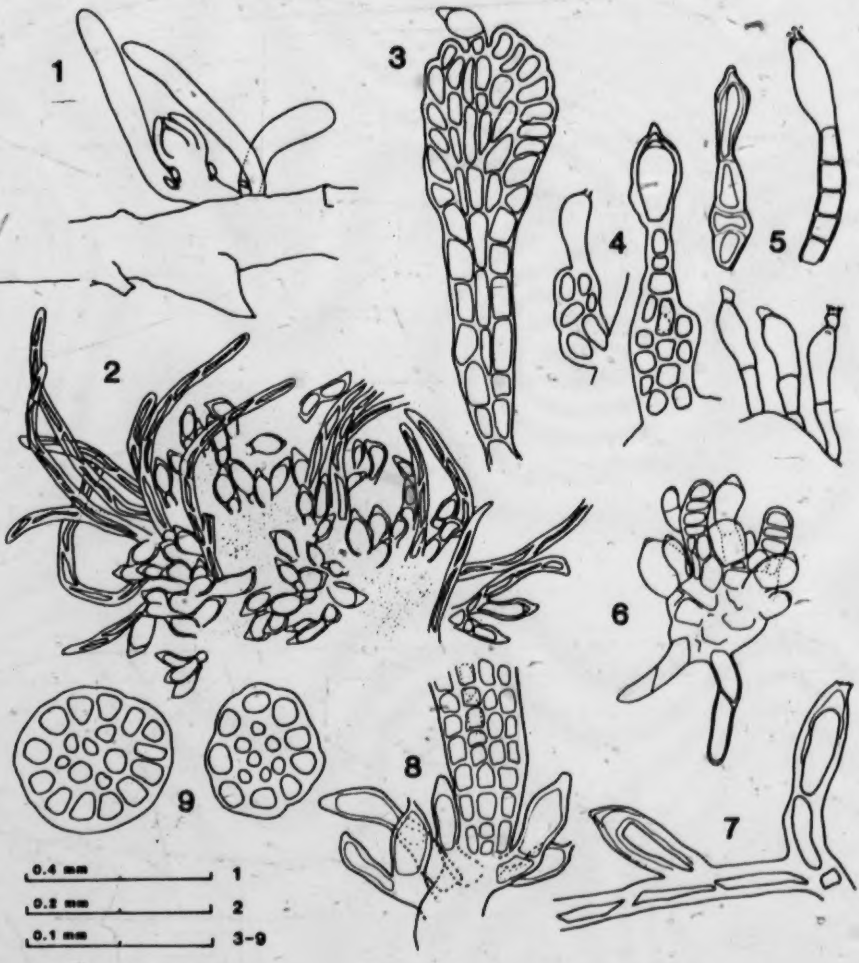
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Figure II-3. Mucilage papillae in Andreaeobryum macrosporum. -- 1 & 2. Axillary hairs. -- 3-6. Rhizoidal papillae (clavate) and rhizoids (cylindric). Bar scale = 25 µm. (Alaska, ALA. 1, SEM & 2, LM: Batten 75-43; 3 & 4, SEM: Murray 8753; 5 & 6, SEM: Murray 6482.)

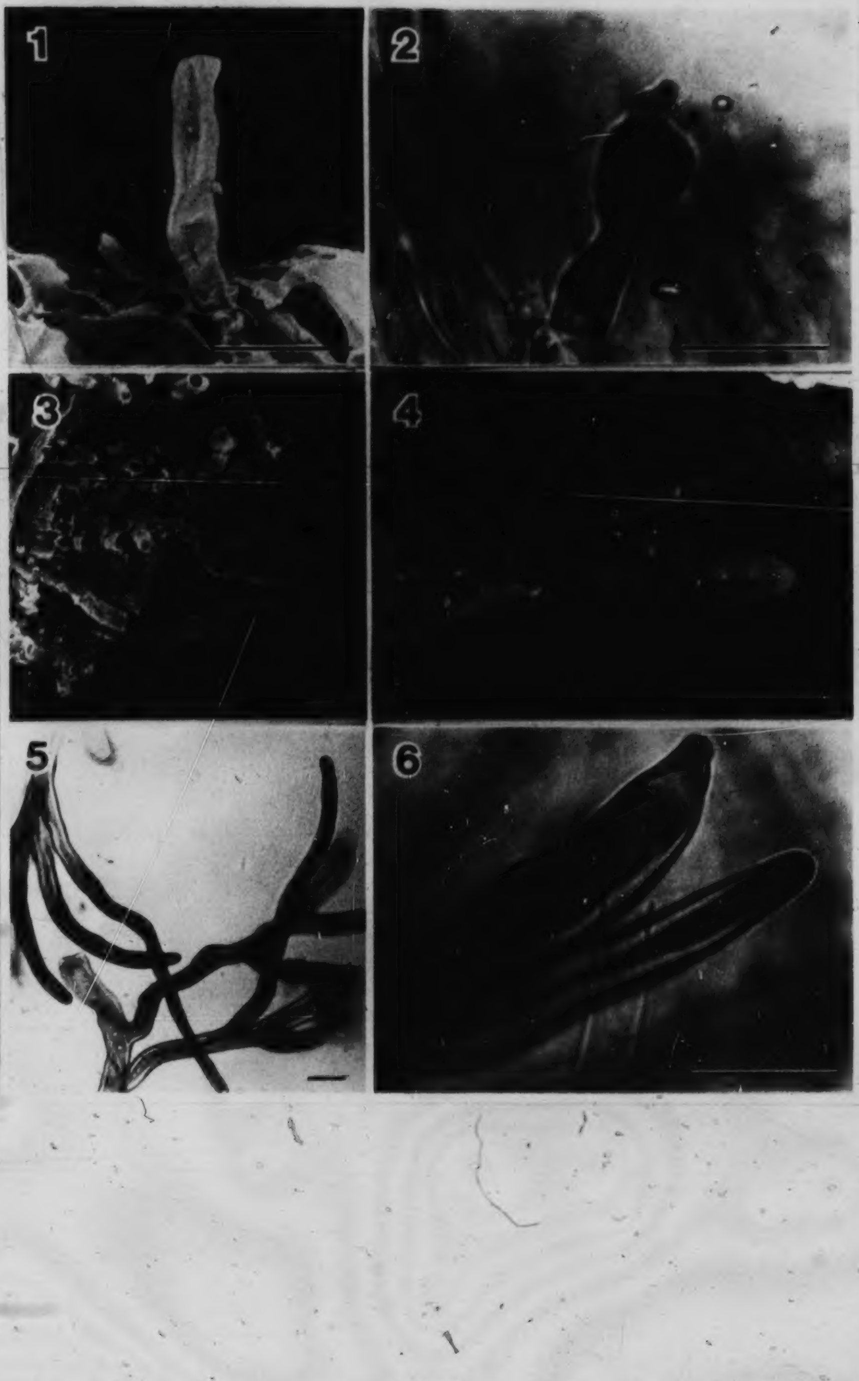
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Figure II-4. Axillary mucilage hairs in Andreaea. Bar scale = 25 µm. (Scotland. 1 & 2, A. megistospora B. Murr. ssp. megistospora: 1, SEM: 31 July 1984, Murray & Perry s.n., ALA; 2, LM: 31 Oct. 1982, Murray & Long s.n., isotype, ALA; 3 & 4, LM, A. rothii Web. & Mohr ssp. falcata [Schimp.] Lindb.: Sep. 1856, Nichols s.n., BM.)

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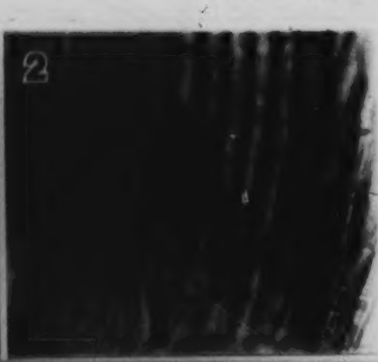
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Figure II-5. Illustrations of Andreaeobryum and Andreaea. -- 1 & 2. Diagrammatic longisections of sporophytes and calyptrae, 1, Andreaeobryum, 2, Andreaea. -- 3. Transection of portion of valve in Andreaeobryum macrosporum. -- 4. Transection of portions of two valves and intervening suture cells in Andreaea (A. nivalis Hook.). (3, Alaska, Batten 75-43, ALA; 4, Canada, Halbert 3888, UBC; see also Figure II-9: 3.)

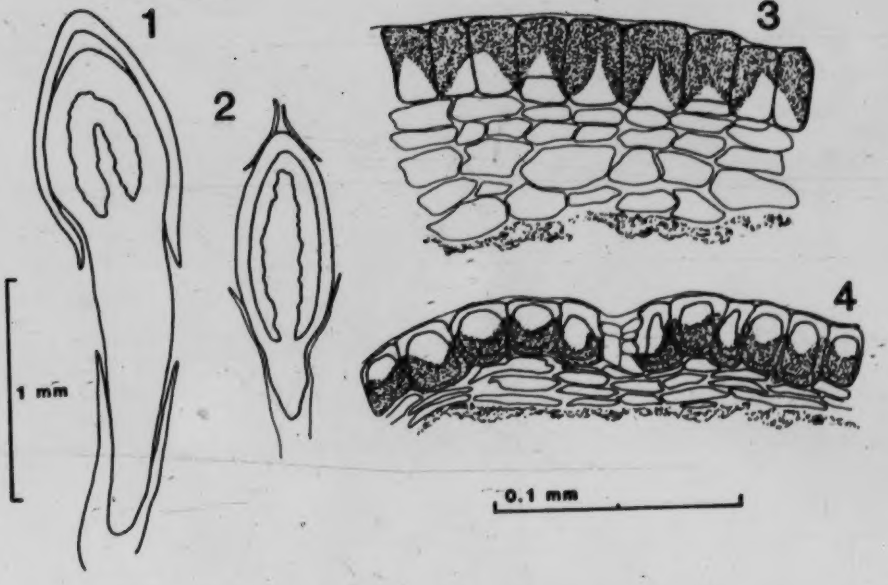
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Figure II-6. SEM photographs of Andreaeobryum macrosporum sporophytes. -- 1. Calyptra on immature capsule, leaves dissected to reveal seta. -- 2-4. Mature sporophytes showing 2, seta ringed by numerous perichaetial bracts, 3, apical tissue disintegrated and valves free, and 4, twisted and flattened seta and capsule base. --5 & 6. Views from above showing capsule assymetry and irregularity of valves, note opacity of epidermal cells due to very thick black outer walls; 5, a 5-valved capsule, 6, an irregularly 4-valved capsule. Bar scale = 250 μm. (Alaska, ALA. 1-4, 6: Batten 75-43; 5: Murray 6713, isotype.)

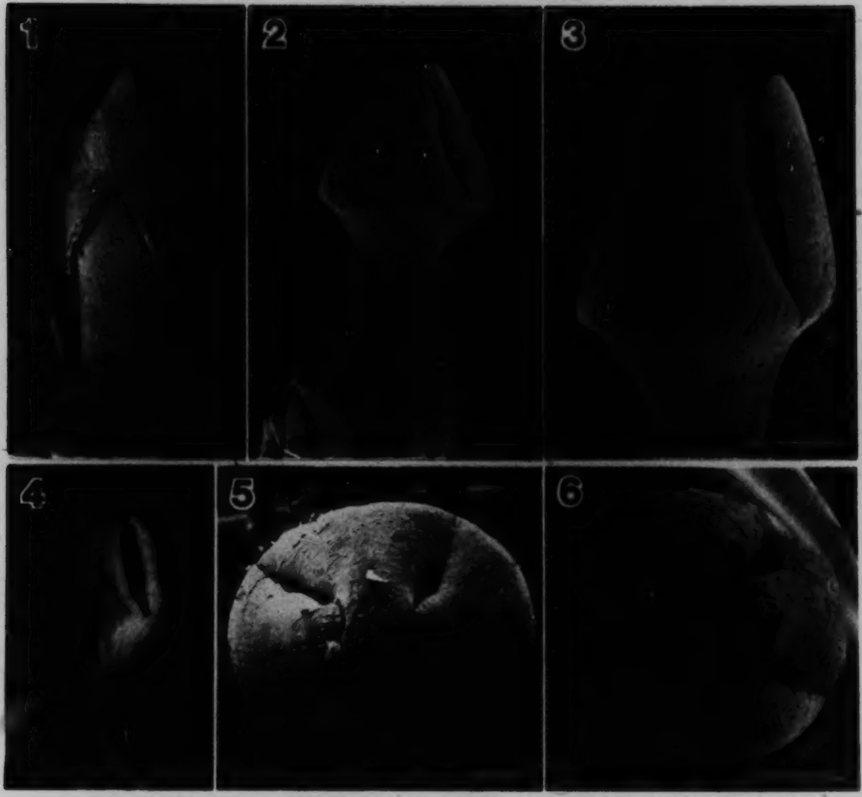
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Figure II-7. SEM photographs of Andreaea sporophytes. -- 1. Calyptra at apex of mature capsule (A. obovata Thed.). -- 2. Capsule dehiscence, capsule contracted in length and valves bulging (A. megistospora B. Murr. ssp. megistospora). -- 3 & 4. Views from above showing typically symmetric capsules with 4 valves, note visibility of epidermal cells (A. sinuosa B. Murr.). Bar scale = 250 μm. (1, Norway, 20 July 1984 Murray s.n., ALA; 2, Scotland, 31 July 1984, Murray & Perry s.n., ALA; 3 & 4, Canada, Schofield 74208, holotype, UBC.)

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Figure II-8. LM photographs of epidermal cells of valves in *Andreaeobryum macrosporum*. -- 1-3. Transections, outer surface upwards, showing pigmented thickenings on outer walls of epidermal cells, inner walls thin; 2 & 3, inner cell layers collapsed with age. -- 4 & 5. Surface views of quadrate to short-rectangular epidermal cells, 4, inner surface, and 5, outer surface, note (at right) irregular edge of valve. Bar scale = 25 μm. (Alaska, ALA. 1-3: *Murray 6713*, isotype; 4: *Batten 75-41*; 5: *Batten 75-43*.)

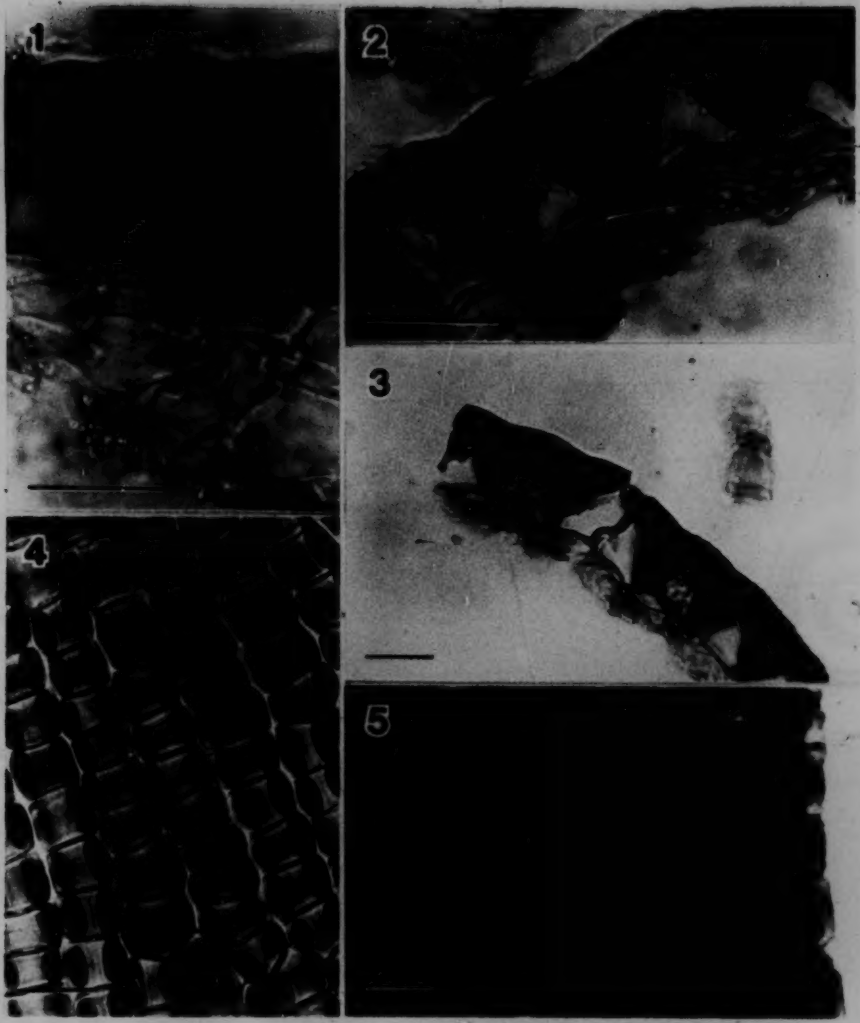
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Figure II-9. LM photographs of epidermal cells of valves in *Andreaea* (1-3: *A*. *nivalis*; 4: *A*. *wilsonii* Hook. f.; 5 & 6: *A*. *frigida* HÜb.). -- 1-4. Transections, outer surface upwards, showing suture cells and pigmented thickenings on inner walls of epidermal cells, inner cell layers collapsed with age, 2, a detail of area near arrow in 1; 3, is drawn in Figure II-5: 4. -- 5 & 6. Surface views of rectangular epidermal cells, 5, inner surface, note porelike thinnings near transverse walls, 6, outer surface. Bar scale = 25 µm. (1-3, Canada, *Halbert* *3888*, UBC; 4, Chile, *J*. *D*. *Hooker* *108*, ALTA; 5 & 6, Czechoslovakia, *Wihan* in Bauer, Musc. Eur. Am. Exs. 2002, NY.)

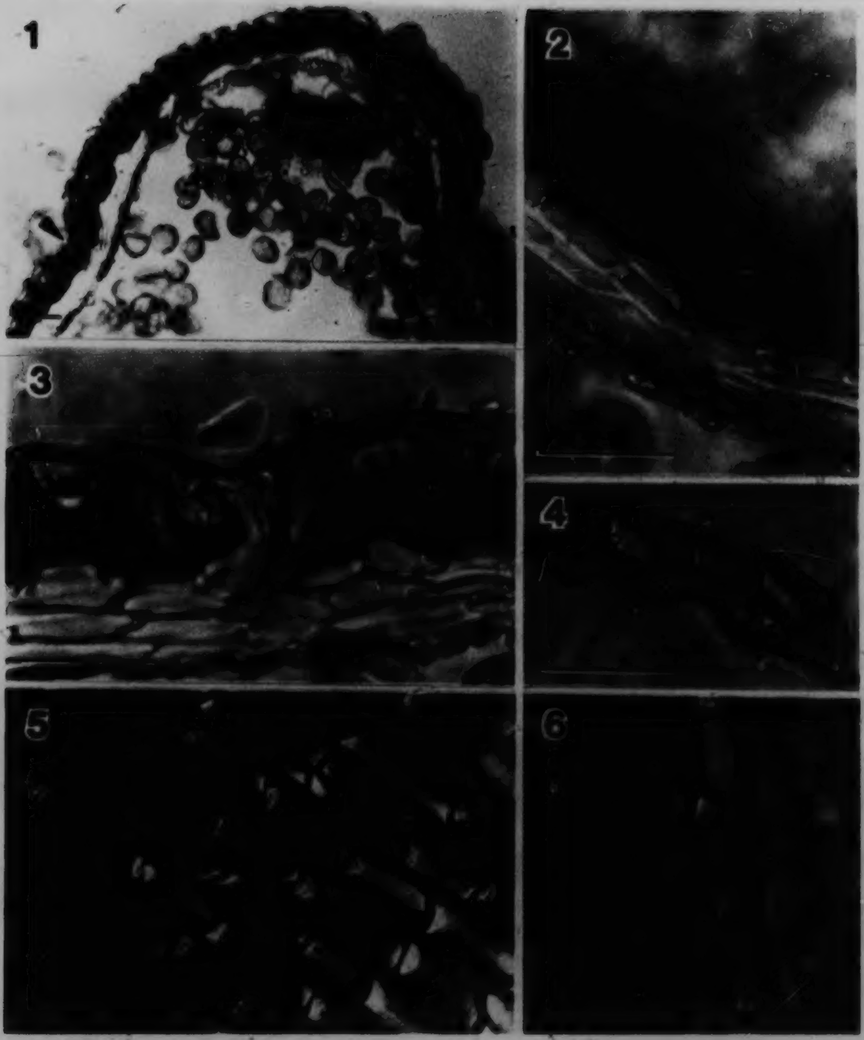

1
2
3
4
5
6

Figure II-10. Distribution of *Andreaeobryum macrosporum*.

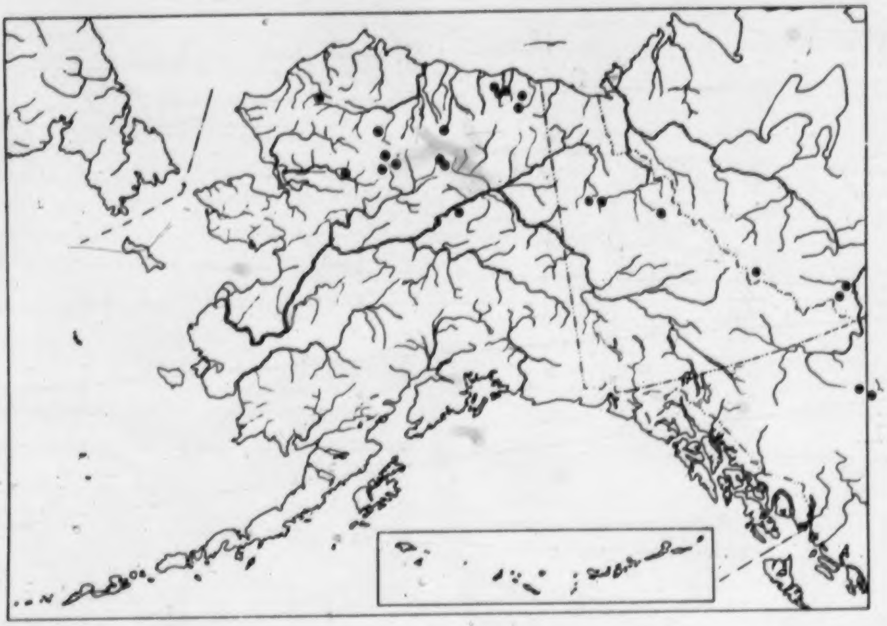
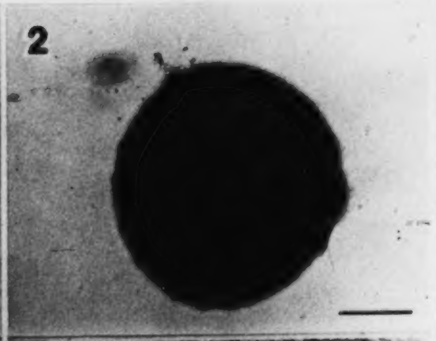


Figure II-11. Andreaeobryum macrosporum spores. -- 1. One turgid living spore, two shriveled dead spores, in tetrad. -- 2-6. Spore ornamentation at different scales; 6, enlargement of portion shown by arrow of 5. 1-3 & 5, bar scale = 25 µm; 4 & 6 bar scale = 10 µm. (Alaska, ALA. 1 & 2, LM: Murray 6713, isotype; 3-6, SEM: Batten 75-43.)

1


2

3

4

5

6

Figure II-12. Illustrations of Andreaeobryum macrosporum. -- 1 & 2. Transections of young seta. -- 3 & 4. Transections of old seta, central cylinder collapsed and seta flattened. -- 5. Seta cells, surface view. -- 6. Transection of stem showing inserted foot with transfer cells. -- 7. Transection of middle part of calyptra. -- 8. Transection of lower part of capsule below valves. -- 9-11. Spores, 9, tetrad showing spore abortion, three dead and one living spores, 10, stretched spore coat with reticulate, patchy ornamentation and 11, germinated spore showing endosporic cell mass, irregular dehiscence and germ tubes. (Alaska, ALA. 1, 2, 6, 7 & 9-11: Batten 75-43; 3-5 & 8: Murray 6713, isotype.)

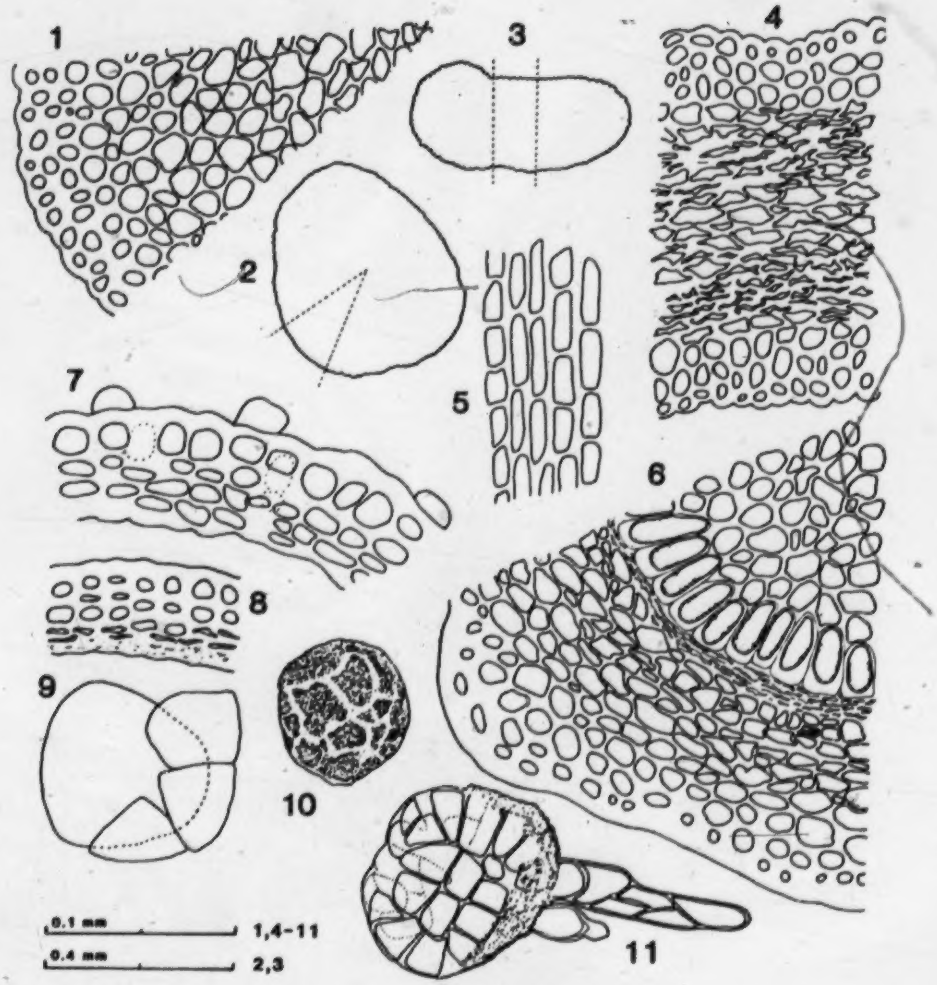

1
2
3
4
5
6
7
8
9
10
11
0.1 mm
1,4–11
0.4 mm
2,3

Figure II-13. Illustrations of Andreaeobryum macrosporum. -- 1. Habit, showing dense protonemal mat and abrupt transition from juvenile to mature leaves. -- 2. Cells in upper part of leaf. -- 3. Cells in lower part of leaf. -- 4. Transections of upper parts of leaves. -- 5. Transections of lower parts of leaves. -- 6. Stem transection. -- 7. Mature leaves. -- 8. Perigonial bract, antheridium and paraphyses. -- 9. Juvenile leaves. (Alaska, ALA. 1-5 & 7: Murray 5068; 6, 8 & 9: Batten 75-43.)

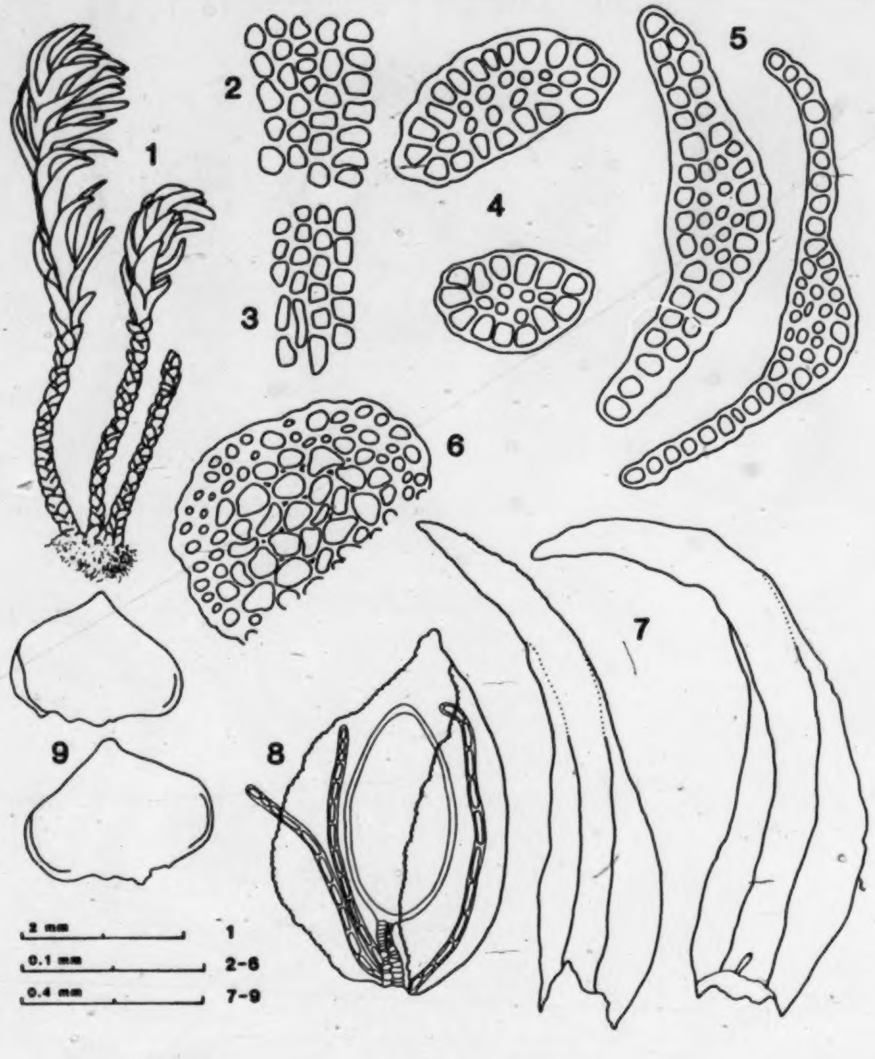

2 mm 1
0.1 mm 2-6
0.4 mm 7-9

Figure II-14. Perichaetial development in Andreaeobryum macrosporum. -- 1. Numerous leaf initials around fertilized archegonium, note also mucilage papillae. -- 2. Numerous bracts and several bracteoles attached to basal stem tissue -- 3. Young bracts developing around fertilized archegonium. -- 4. Expanded receptacle and sporophyte within papillose calyptra; numerous mounds formed on stem from which mucilage papillae and bracts emerge. -- 5. Transection of expanded receptacular tissue in region of foot. -- 6. Bracteoles with apical mucilage papillae. -- 7. Bracts, variable in shape and size, some lobed or appearing fused. (Alaska, ALA. 1-3 & 5-7: Murray 5068; 4: Batten 75-43.)

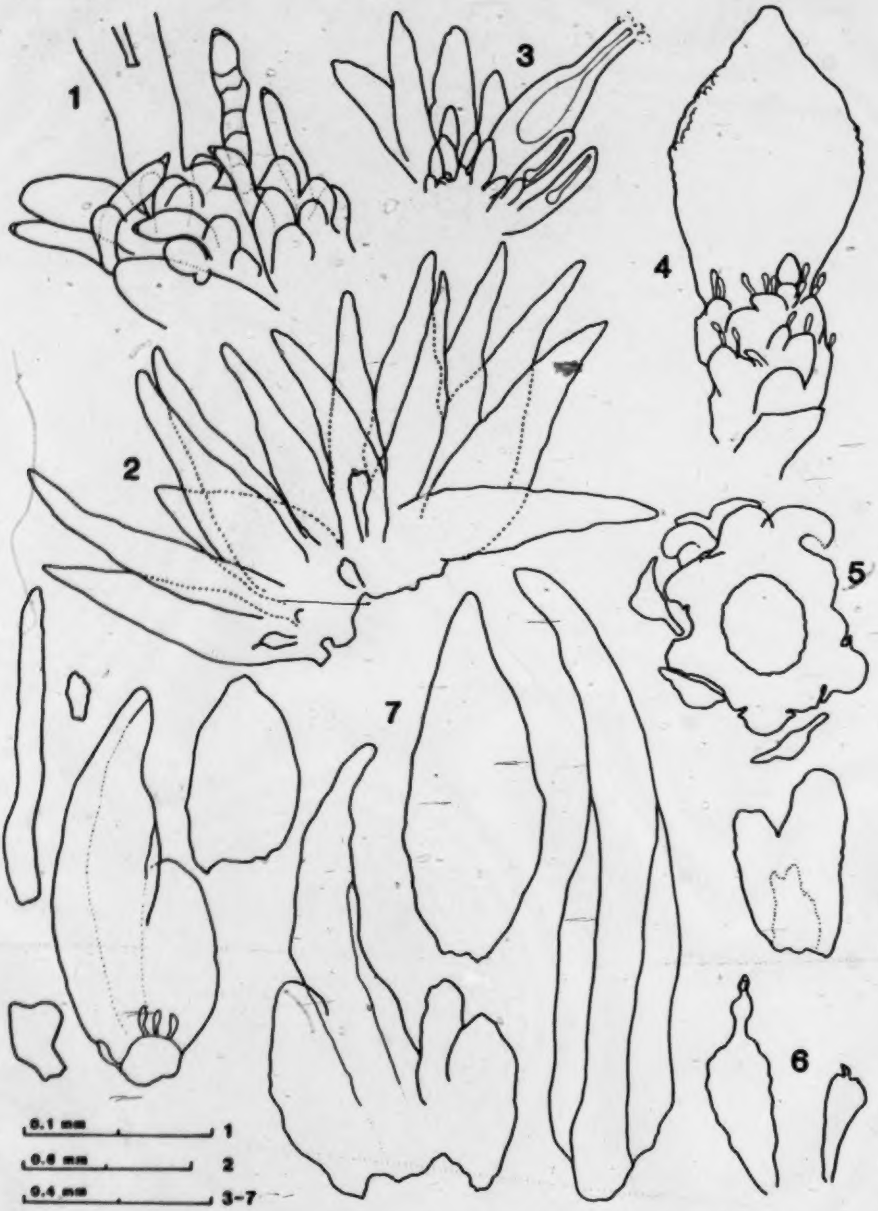
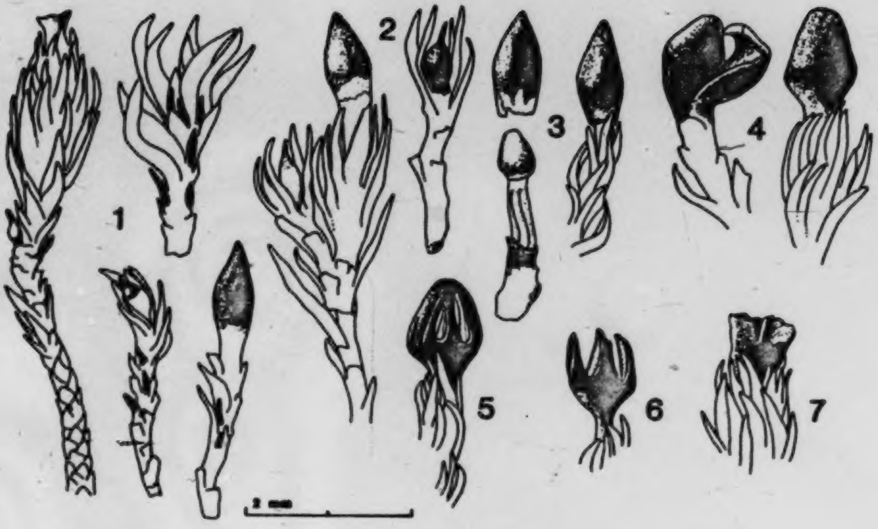

0.1 mm 1
0.6 mm 2
0.4 mm 3-7

Figure II-15. Sporophyte development in Andreaeobryum macrosporum. -- 1. Lateral archegonia and terminal sporophytes. -- 2. Immature sporophytes within calyptrae. -- 3. Immature sporophyte, calyptra removed to show capsule (spores already brown at this stage) and massive seta. -- 4. Almost mature capsule, showing unusual basal attachment of calyptra. -- 5. Mature capsule, note irregular valves. -- 6. Old capsule, valves free due to disintegration of apical tissue. --7. Old capsule base, valves broken off, columella persistent, note dense whorls of perichaetial bracts. (Alaska, Batten 75-43, ALA.)


2 mm

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III. ANDREAEA SINUOSA, SP. NOVA, FROM ALASKA, BRITISH COLUMBIA AND SCOTLAND[1]

During monographic study of the genus Andreaea, I found several collections, most named A. rupestris Hedw., that represent a new species.

Andreaea sinuosa B. Murray, sp. nova (Fig. III-1)

Parva, ecostata; folia anguste lanceolata, margine incurvata; sporae parvae, 11-21 µm diametro. Haec species differt ab omnibus ecostatibus congeneribus parietibus sinuosis cellularum laminae, similibus generi Racomitrio.

Plants small, densely tufted but easily broken, green-brown, red-brown, purple-black or black; saxicolous. Protonemata persistent, consisting of stolon-like, yellowish, multiseriate filaments and uniseriate, brown rhizoids; thallose appendages rarely seen. Stems erect, rarely over 10 mm high, simple to sparingly branched, red-brown, cells frequently sinuose in surface view; in transverse section round, with round, thick-walled cells, central strand absent, outer cells usually slightly smaller than inner, with exterior walls bulging. Axillary hairs frequent, persistent, with 1 (rarely more) brownish, quadrate to short-rectangular basal cell and 1 (rarely more) at first hyaline, later brown, cylindric or clavate terminal cell, with breaks in thin outer wall. Scale-leaves frequent along lower stems, minute, about 0.25-0.30 mm long, lanceolate to ovate, apiculate, occasionally sparsely toothed from projecting cells. Leaves spirally arranged, sometimes appearing tristichous, larger distally, when moist slightly spreading, when dry erect, more or less appressed; narrowly lanceolate to linear-lanceolate, slightly curved to secund, acute or occasionally rounded, to 1.6 mm long, unistratose or with occasional small marginal or laminal bistratose areas; lamina about 22-28 μm thick distally, 15-20 μm thick proximally; bases oblong, slightly sheathing, narrowed to the straight insertion, usually strongly gibbous on one side only and with a conspicuous fold; margins conspicuously incurved from bases to apices, entire. Costa absent. Upper leaf cells irregularly rounded, oval or oblate, 10-14(16) μm long, 10-12 μm wide, with large, low, brown to white papillae that are more numerous centrally than marginally or apically; walls ± incrassate and collenchymatous, with micropapillae often visible in transverse section due to bulging of walls between adjacent cells. Laminal cells gradually larger and conspicuously pitted to sinuose towards the sheathing base, with papillae over lumina sparse and micropapillae over transverse walls between cells more conspicuous. Basal cells rectangular to oblong, 22-50 μm long, 10-12 μm wide, lumina often scalariform, longitudinal walls incrassate, pitted and strongly sinuose, as in Racomitrium, transverse walls thin; luminal papillae absent, transverse wall micropapillae frequently visible in transverse section. Sexual condition undetermined, apparently dioicous, but stems very short and fragile, so possibly cladautoicous. Perigonia lateral or terminal but often appearing lateral due to renewed stem growth, bud-like, leaves ovate, about 0.8 mm long, cells not sinuose; antheridia usually 3-4, about 0.3-0.4 mm long, paraphyses few or lacking, with biseriate areas distally. Perichaetia terminal or appearing lateral due to renewed stem growth, inner perichaetial leaves ovate-oblong, convolute and sheathing, outer less sheathing, apiculate, to 2 mm long; archegonia lateral or terminal, usually 4-6(8), sometimes solitary in leaf axils, about 0.2 mm long. Sporophytes usually present, mature in summer; overwintering as immature capsules within perichaetia; very young green, pre-meiotic capsules seen in June and September collections from British Columbia. Capsules barely emergent to shortly exserted on pseudopodia; erect, when wet or immature ovoid, about 0.8 mm long, when mature and dry valves bulging; valves 4, brown-black; valveless capsule base tan to brown, usually occupying 1/2 or more of the capsule length. Calyptrae apical, small, campanulate-mitrate, rostrum consisting mainly of unmodified archegonial neck; often falling early. Spores round, small, (11)13-19(21) μm, brown, finely papillose to striate-reticulate-papillose; spore abortion rare, two shriveled and two turgid spores seen rarely in tetrads; germination precocious, few cells, 2-4, formed within spore wall, sometimes prior to dehiscence.

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[1] A version of this chapter has been published. Murray, B. M. 1986 [1987]. Bryologist 89: 189-194.

Type: CANADA. BRITISH COLUMBIA: West Vancouver, Cypress Bowl area, Crest Trail toward The Lions, ca. 49°20'N, 123°10'W, boulder in late snow area, 13 September 1979, W. B. Schofield 74208 (holotype, UBC).

Additional specimens examined: USA. ALASKA: Aleutian Islands: Attu I., vic. of Massacre Bay, 52°50'N, 173°14'E, Jormia Pass, 11

November 1945, *Howard 597* (MICH). CANADA. BRITISH COLUMBIA: Queen Charlotte Islands: Graham I., Mt. Brown, 16 August 1985, *Schofield & Spence 84073* (UBC). Vancouver I., Mt. Cain, N of Schoen L., 50°14'N, 126°20'W; 12 September 1970, *Halbert & Price 6802* (UBC). North Vancouver, Mt. Seymour; 20 June 1961, *Schofield 14561* (UBC), 27 October 1962, *Schofield 20215* (UBC), 14 September 1968, *Schofield 37892* (UBC). West Vancouver, Cypress Bowl Provincial Park, 49°22'N, 123°12'W, 19 June 1980, *van Velzen & Leong relevé 118*, *relevé 124* (UBC). UK. SCOTLAND: East Ross (Vice-county 106): Beinn Dearg, 18 km SE of Ullapool, grid reference 28/26.81, *Coppins et al. ex Coppins 10534* (E), also *Coppins et al*. (E Lichen Herbarium, under *Lecidella bullata* Körb., *Coppins 10534*; *Lecidea griseoatra* (Flot.) Schaer., *Coppins 10523*; and *Lecanora leptacina* Sommerf., *Coppins 10524*). South Aberdeen (Vice-county 92): Beinn a'Bhuird, below S Top, grid reference 37/095.977, *Murray & Long*, 13 July 1985 (ALA), *Long & Murray 12791* p.p. (E); Westerness (Vice-county 97): Ben Alder Forest, Geal-charn, grid reference 27/477.748, *Gilbert, Fox & Purvis*, 9 July 1981 (BM Lichen Herbarium, under *Lecanora leptacina* Sommerf.).

Distribution (Fig. III-2). *Andreaea sinuosa* is very rare, known only from the localities cited. In Alaska, *A. sinuosa* is known only from the westernmost island of the Aleutians, Attu, about 750 km from the Asian mainland. Of hundreds of specimens of *Andreaea rupestris* examined from British Columbia and the British Isles, I found but a handful referable to *A. sinuosa* from southwestern British Columbia and none from the British Isles. Scottish material was found serendipitously while I was studying lichens growing on *Andreaea* with B. J.

Coppins, Royal Botanic Garden, Edinburgh. A subsequent trip with D. G. Long to a late snow-patch in Scotland and further examination of snow-bed species at the Lichen Herbarium at BM yielded two more collections. It is likely, however, that the species occurs in other regions with similar climates and habitats (see below). Undoubtedly, it will be found along the North Pacific Arc between its presently known sites in Attu Island and British Columbia, and it may well occur in other oceanic parts of Europe and in Asia.

Andreaea sinuosa can be added to the list of about 40 bryophytes that are disjunct between western North America and Europe. This element has been discussed mainly by Schofield (1980) and by Schuster (1983), who cited most relevant literature and many examples. This pattern has received little attention compared to that given bryophytes disjunct between eastern North America and eastern Asia, although, as Schofield pointed out, the latter element involves about half as many taxa. Andreaea sinuosa is one of the western North American-western European disjuncts that occurs in oceanic regions and is rare throughout its range. Schofield and Schuster both consider many of the taxa in this element to be Tertiary relicts whose ranges were sharply contracted because of changes in climate and vegetation during the Quaternary. This view is shared by Ratcliffe (1968) and Corley (1983) in their discussions of British bryophytes belonging to the North Atlantic group, which includes oceanic northwestern North American-northwestern European disjuncts. Ratcliffe (1968) discussed several North Atlantic species that flourish in late snow-bed vegetation in the Cairngorms. Like these, Andreaea sinuosa grows today in essentially periglacial conditions and could have survived in refugia during glacial intervals.

Ecology. *Andreaea sinuosa* occurs on acidic rock in mountainous regions with a humid temperate climate. It has been found at elevations of about 150-300 m in the Aleutians, 550-1500 m in the subalpine and alpine zones of British Columbia and 990-1100 m in the middle alpine zone in Scotland. The latitudinal range is about 49-53°N in Alaska and British Columbia and 57-58°N in Scotland. The habitat of the Alaskan collection is not known. In British Columbia five collections are labeled as from dry, exposed boulders and outcrops, one is from a shaded face of a boulder, and one is from a boulder in an area of late-lying snow. According to W. B. Schofield (personal communication 1986) all of the British Columbia localities are in late-lying snow areas.

Andreaea sinuosa is a snow-bed specialist in Scotland where the lichens *Lecanora leptacina*, *Lecidella bullata*, *Lecidea griseoatra*, and *Lecidea* sp. are close associates, sometimes overgrowing *A. sinuosa*. These lichens are apparently restricted to snow-beds in the Cairngorms (Gilbert & Fox 1985). The most constant snow-bed species, *Lecanora leptacina*, was associated with *A. sinuosa* in all three Scottish localities and also occurred in the two British Columbia collections in which lichens were seen. *Lecidella bullata* and a lichen tentatively referred to *Lecidea* s. lat. by B. J. Coppins (in litt. 1986) were found in one Scottish and one British Columbia collection of *A. sinuosa*.

Associated *Andreaea* species are *A. rupestris* var. *rupestris* and *A. blyttii* Schimp. in both British Columbia and Scotland and *A.*

heinemannii Hampe & C. Müll. (= A. angustata Lindb. ex Limpr.) in British Columbia. Andreaea rupestris is widespread, and A. blyttii is primarily a circumarctic-alpine species with interrupted range, but it also occurs on exposed rocks in subalpine areas in western North America. It grows where snow persists, often in the zone of very late-lying snow. Andreaea heinemannii has been considered endemic to southern Europe and the Canary Islands (Schultze-Motel 1970 as A. blyttii ssp. angustata (Lindb. ex Limpr.) Schultze-Motel), but I have found it to be wider ranging, occurring from the Arctic in Greenland to the mountains and forests of Europe, the Caucasus, Madeira and western North America. It occurs from near sea level in the Arctic to about 4175 m in Colorado, usually growing on dry exposed rock, sometimes near glaciers and in snow-beds. Most Andreaea species occur in habitats with seasonal extremes of moisture and tolerate extreme desiccation as well as submergence. Snow-bed species have a short growing season and are seasonally submerged, but after the snow melts they may be very dry and exposed. Lack of competition in such sites could also be a factor affecting their distribution. Andreaea sinuosa, A. blyttii and A. heinemannii usually have very short stems and are little branched, likely a response to a short growing season. The pH range of A. sinuosa is unknown, but based on information on the pH of snow-bed soils where some of its associates grow, it may well prove to be an extreme acidophile. Gilbert & Fox (1985) recorded that the extreme snow-bed soils in the Cairngorms had a pH in the range of 4.2-4.4. Further circumstantial evidence comes from the work of Elvebakk (1984) on siliceous boulder snow-beds on Svalbard. Andreaea blyttii (cited above as an associate of A. sinuosa) grew there on rocks with a mean mineral soil pH of 4.8. Andreaea sinuosa should be sought among herbarium specimens of the snow-bed lichens mentioned above, especially Lecanora leptacina, and looked for near glaciers and snow-beds among other Andreaea species.

Differentiation and Relationships. Andreaea sinuosa is one of the smallest and least variable species in the genus. The major feature differentiating it from all other ecostate Andreaeae is the strongly sinuose basal cell walls (the basis for the epithet). Strongly sinuose cell walls occur elsewhere in mosses only in the Grimmiaceae, and Noguchi (1974) has suggested that the sinuose wall structure in the genus Racomitrium is an adaptation to dryness. Andreaea sinuosa also differs from the majority of Andreaea species in its small spores, less than 21 µm in diameter. The species with which it has been, and is likely to be, confused in the field is the polymorphic A. rupestris. Andreaea sinuosa, however, has narrower, less sheathing leaves, with the margins strongly incurved to the apex. The following key differentiates A. sinuosa from other ecostate North American (north of Mexico) and European Andreaeae.

Key to Ecostate Andreaeae
of North America (North of Mexico) and Europe

1. Basal leaf margins denticulate. Northwestern Europe and southern Greenland .... A. alpina Hedw.
1. Basal leaf margins entire or weakly crenate 2
2. Most spores less than 21 µm 3
2. Most spores over 24 µm or spores absent 4

3. Basal marginal cells mostly rectangular. Basal cell walls strongly pitted and sinuose .... _A_. _sinuosa_

3. Basal marginal cells all quadrate. Basal cell walls little pitted, never sinuose. New to Northern Hemisphere (including British Columbia, Britain, France and Spain) .... _A_. _mutabilis_ Hook. f. & Wils.

4. Basal marginal cells all quadrate .... _A_. _mutabilis_

4. Basal marginal cells mostly rectangular, occasionally some quadrate 5

5. Leaves narrowly lanceolate. Cell walls strongly pitted and sinuose .... _A_. _sinuosa_

5. Leaves lanceolate or panduriform. Cell walls strongly or weakly pitted, not sinuose 6

6. Leaves usually curved to secund, with oblique apices. Papillae usually prominent and whitish, at least dorsally on upper leaves. Upper cell lumina often stellate, rounded or oval; walls usually incrassate, pitted, and collenchymatous. Plants green-bronze, black or reddish 7

6. Leaves usually straight, apices occasionally oblique. Papillae usually low or absent, very rarely prominent or whitish. Upper cell lumina rounded or stellate; walls incrassate, pitted, and collenchymatous or not. Plants characteristically brown, black, or reddish black 8

7. Leaves lanceolate or occasionally panduriform, gradually narrowed to short or long, obtuse or acute apices. Usually on rock. Widespread .... _A_. _rupestris_ var. _rupestris_

7. Leaves abruptly narrowed from ovate or panduriform bases to long acute apices. On rock or soil. Primarily northern .... A. rupestris var. papillosa (Lindb.) Podp.

8. Leaves usually asymmetric, ± lanceolate, broadest below mid-leaf, not apiculate. Papillae inconspicuous. Basal cells short-rectangular; lumina broad and bulging, walls little pitted. Upper laminae unistratose or some leaves with bistratose patches; cell lumina rounded, walls not very collenchymatous or incrassate. Plants black or brown, occasionally reddish black. Primarily northern .... A. alpestris (Thed.) Schimp.

8. Leaves symmetric, panduriform, broadest above mid-leaf, ± apiculate. Papillae rarely conspicuous. Basal cells rectangular to long-rectangular; lumina rarely bulging, walls pitted. Upper laminae unistratose; cell lumina stellate, walls collenchymatous and incrassate. Plants usually reddish or purple-black, occasionally black. When submerged in running water, greenish and with distant, often secund leaves. Primarily northern .... A. obovata Thed.

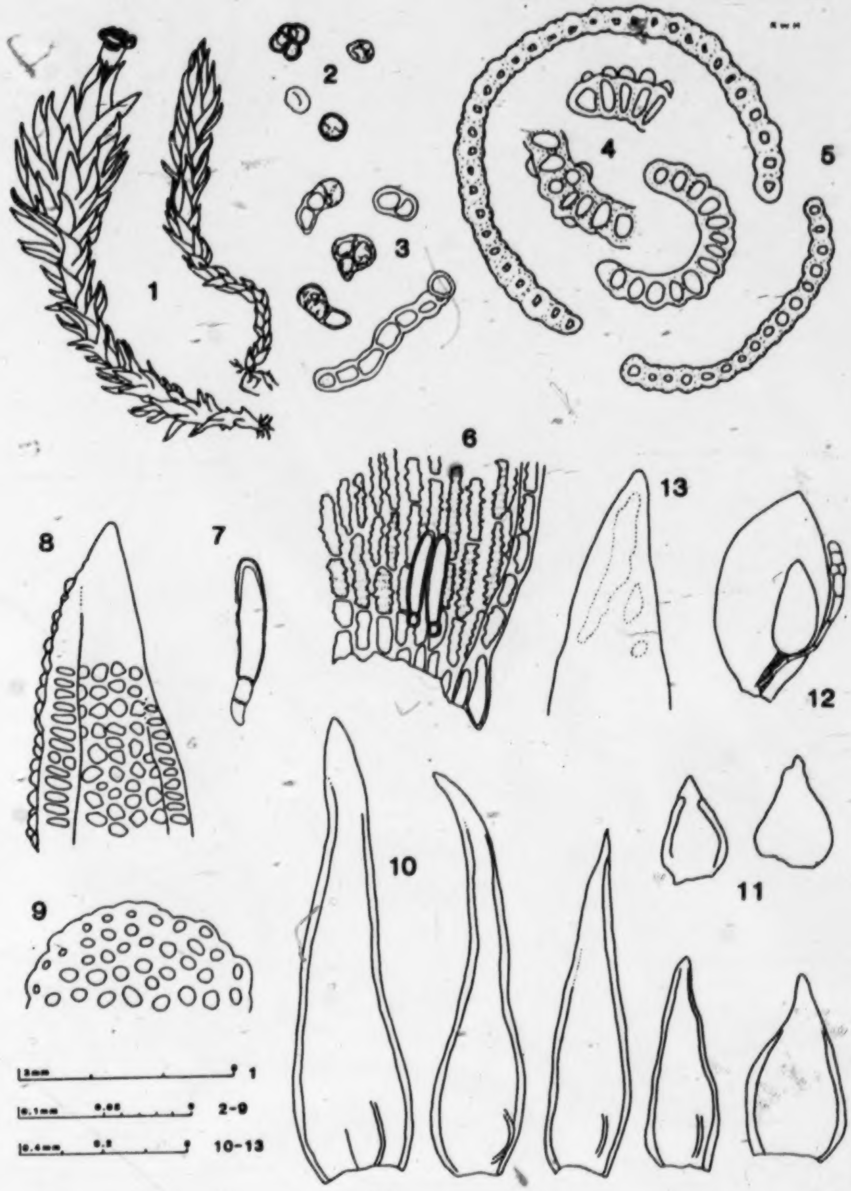
Andreaea sinuosa does not appear to be closely related to other ecostate species, none of which has leaves with sinuose cell walls. It is not part of the A. rupestris complex (including A. alpestris and A. obovata), which has pitted to nodose but non-sinuose walls, few persistent axillary hairs, frequent spore abortion, and medium-sized spores. Andreaea sinuosa does, however, share several features with most costate Andreaeae in section Nerviae Card. ex Broth.: sinuose walls, numerous persistent axillary hairs, and infrequent spore abortion.

Traditionally, most *Andreaeae* with differentiated, convolute perichaetial leaves have been separated into two groups depending on the presence (in section *Nerviae*) or absence (in section *Andreaea*) of a costa. Transitional taxa occur, however. For example, *A. marginata* Hook. f. & Wils., although clearly related to an ecostate species, *A. alpina*, has a long subula in which all but the marginal cells are in two (rarely four) layers, and it could be considered to have a weak costa. And certain forms of *A. heinemannii* (in section *Nerviae*) are essentially ecostate with a subula consisting of two layers of undifferentiated cells and a unistratose leaf base. Sinuose cells just like those in the ecostate *A. sinuosa*, occur frequently in the costate *A. heinemannii*. *Andreaea sinuosa* could represent another transitional form, having leaves with occasional bistratose portions, in addition to the features mentioned above. These cases, and others, suggest that the commonly accepted distinctions are artificial, that close relationships occur across the traditional sections, and that a re-evaluation of the definition and taxonomic significance of the costa is necessary in the genus *Andreaea*.

Acknowledgements

I am very grateful especially to D. G. Long for guidance in the field and help at E and to B. J. Coppins for lichen identifications and assistance at E; to D. F. Murray and A. R. Perry for criticism, to D. H. Vitt for criticism and the base map, to W. B. Schofield (UBC), P. W. James (BM), H. A. Crum (MICH), and O. L. Gilbert for information about, access to, or loan of specimens. Kay W. Holmes made the drawings. Field work was supported by the University of Alaska Museum.

Figure III-1. Illustrations of *Andreaea sinuosa*. Drawn from holotype (*Schofield 74208* UBC) unless noted. -- 1. Habits, leaves moist (left) and dry (right). -- 2. Tetrad and spores. -- 3. Germinated spores. -- 4. Transverse sections near leaf apices (lower two from *Schofield 37892* UBC). -- 5. Transverse sections at leaf bases (lower from *van Velzen & Leong* UBC 20785). -- 6. Leaf base, ventral view, showing cells and axillary hairs. -- 7. Axillary hair, from perichaetium. -- 8. Upper part of leaf showing cells and papillae (from *Schofield 37892* UBC). -- 9. Transverse section of stem. -- 10. Leaves, ventral views, distal to proximal. -- 11. Scale-leaves, ventral and dorsal views. -- 12. Perigonial leaf, antheridium and paraphysis. -- 13. Leaf apex, bistratose portions dashed (from *Schofield 37892* UBC).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0.4mm
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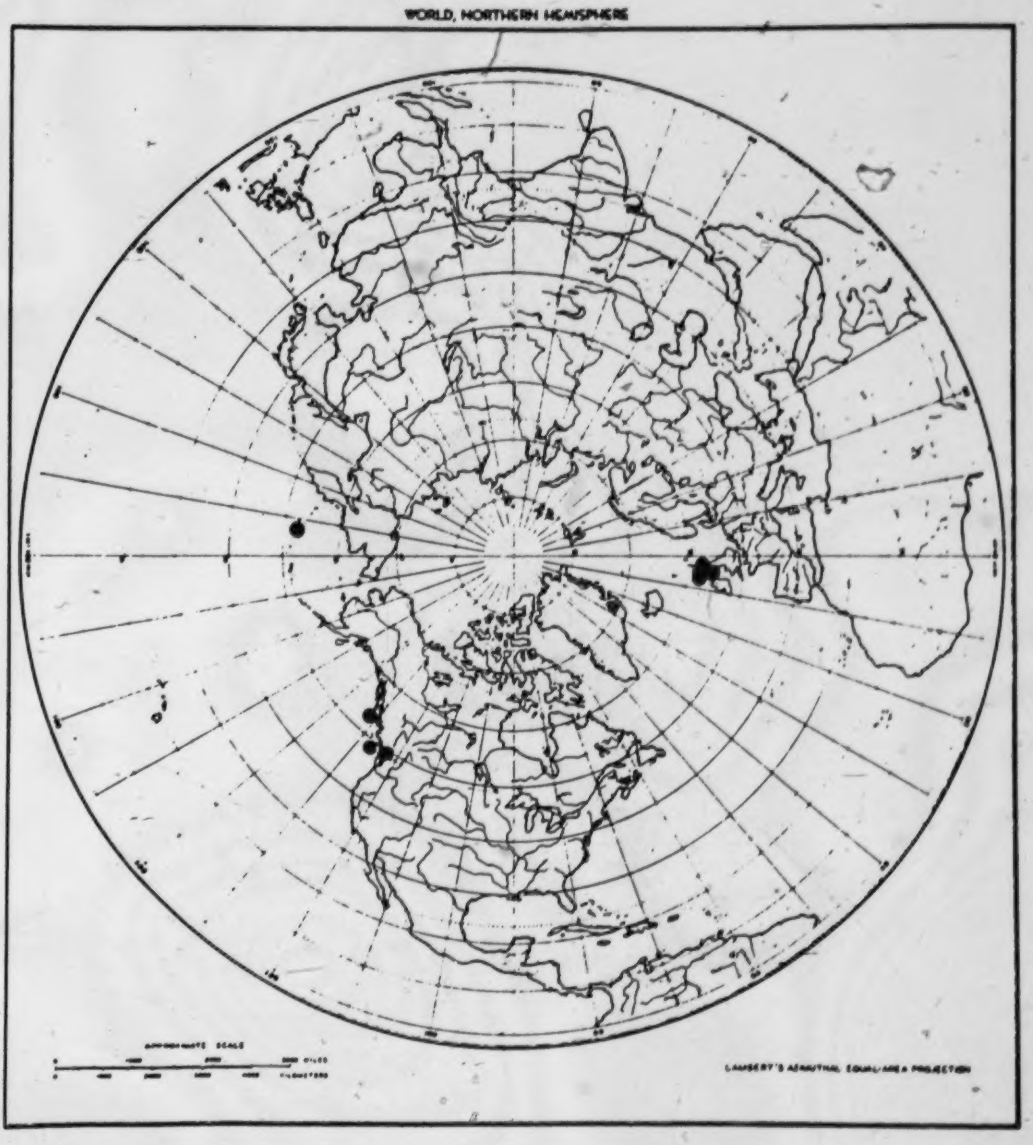
10-13

Figure III-2. Distribution of Andreaea sinuosa.

WORLD, NORTHERN HEMISPHERE


APPROXIMATE SCALE
MILES
KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

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IV. ANDREAEA SCHOFIELDIANA AND A. MEGISTOSPORA, SPP. NOV., AND TAXONOMIC CRITERIA FOR SECT. NERVIAE[1]

Traditionally, leaf characters have been used to differentiate most *Andreaeae*, including members of section *Nerviae* Card. *ex* Broth. (costate taxa with convolute perichaetial bracts), and this approach was followed by Schultze-Motel (1970) in his monograph of costate *Andreaeae*. While studying northern *Andreaeae*, I found that the few specimens from Alaska referable on leaf characteristics to *A. rothii* Web. & Mohr had extremely large spores, some over 100 um in diameter, much larger than any reported for the genus. An examination of North American herbarium material identified as *A. rothii* showed that most western material had very large spores while none of the eastern material did. A survey of my recent collections of *Andreaea* from Scotland revealed that very large-spored material occurred occasionally there as well. These discoveries led me to reassess the taxonomy of section *Nerviae* with special attention paid to the size of spores.

As a result, I have found spore size to be the most useful criterion for taxonomic separation. Traditional characters, such as leaf shape, degree of falcateness, the ratio of costal to laminal width in the upper part of the leaf (limb), and length of the costa tend to vary within taxa. Although useful in delineating species, these characters have been the source of misunderstanding when too much reliance has been placed on them. These features, as well as the papillosity of perichaetial bracts, are sometimes most useful at the infraspecific level.

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[1] A version of this chapter has been submitted for publication.

Material that has previously been treated as *A. rothii* includes three new taxa from northwestern parts of North America and Europe that are described below. A key to costate *Andreaeae* in North America and Europe is provided, and major diagnostic features and relationships of section *Nerviae* are discussed.

Andreaea schofieldiana B. Murray, sp. nov. (Fig. IV-1)

Andreaea sect. *Nerviae*. Parva vel mediocris; folia lanceolata vel sensim contracta e basi oblonga; lamina distali parte folii distincta; costa biconvexa plerumque valde protuberans in pagina dorsali; bracteae perichaetiales intimae interdum papillis parvis sparsis; sporae mediocres, 20-30(36) μm diametro. Haec species differt ab *A. frigida* Hüb. statura minore, sporis minoribus, costa valde biconvexa, habitatione aridiore, ab *A. rothii* Web. & Mohr et *A. megistospora* B. Murr. sporis minoribus et foliis lanceolatis.

Plants small to medium-sized, caespitose, bronze-green, brown to brown-black, juvenile leaves and inflorescences red-brown; saxicolous. *Protonemata* typical of the genus. *Rhizoids* uni- and bi-seriate. *Protonemal appendages* rarely seen, typical of the genus. *Stems* erect to curved, 0.5-1.5(2) cm high. *Axillary hairs* frequent, persistent, with one to many (in perichaetia) basal cells and one to many (in perichaetia) brownish mucilaginous cells. *Primary leaves* (irregularly shaped leaves occurring within perichaetia and at stem and branch bases, resembling the pseudoparaphyllia of pleurocarpous mosses and protonemal appendages of Andreaea) irregularly lanceolate to partly filamentous, sometimes partially bistratose or lobed, usually up to about 0.2 mm long, rarely to 1 mm with fleshy multistratose tip. Juvenile leaves 0.25-0.40 mm long, apiculate, margins often crenate below apiculus. Mature leaves evenly spaced, when moist widely spreading, when dry appressed; straight, curved or secund, lanceolate or sometimes gradually tapering from oblong base, membranous in texture, to 2.2(2.5) mm long, lamina distinct throughout leaf, usually bistratose above, or with large bistratose patches, often unistratose near costa, rarely entirely unistratose; apices acute, bases not or slightly sheathing, slightly narrowed to the straight or slightly decurrent insertion; margins plane, reflexed or slightly incurved, usually conspicuously thickened, often distantly denticulate or crenate due to erosion and irregular production of cells. Costa present, single, distinctly delimited, transition between costa and lamina very distinct; biconvex to terete or at least strongly bulging dorsally; narrow, 1/6-1/4 the width of the leaf base, frequently weak or absent basally in subperichaetial leaves, of equal width throughout length, percurrent or excurrent, sometimes filling the upper limb and forming a fleshy fragile tip possibly serving as a means of asexual reproduction; basal cells on both surfaces elongate with sinuose walls, cells at shoulder slightly papillose, cells above shoulder similar to laminal cells; in transverse section of up to 6 layers, cells little differentiated, innermost 5-6 cells smaller and not green when young. Laminal cells mostly round to oblate, rarely quadrate, 6-12 µm long, 8-12 µm wide, evenly thin-walled, smooth, basal cells especially near costa rectangular and with slightly pitted frequently sinuose walls, marginal cells usually like laminal cells, rarely a few short-rectangular. Cladautoicous. Perigonia lateral or terminal, buds narrow, inner bracts about 0.8 mm long, ± convolute, occasionally denticulate along margins due to papillose cells, with scattered papillae; antheridia usually 4-6, ca. 0.4-0.5 mm long, paraphyses numerous, often branched, usually uniseriate, rarely with biseriate portions. Perichaetial bracts differentiated, ovate-oblong, convolute, to 2.5 mm long, cells often sinuose; inner bracts ecostate, with scattered bistratose portions, occasionally with scattered low papillae, margins crenate; outer bracts costate, with short subulae; archegonia terminal or appearing lateral due to renewed stem growth. Sporophytes common, mature in early summer. Capsules exserted on pseudopodia; about 1.0 mm long, valves 4(5-6), valveless capsule base usually occupying less than 1/3 of the capsule length. Calyptrae typical of the genus. Spores round or angled, 20-30 μm (to 36 μm, when germinated) finely papillose to striate-reticulate-papillose; spore abortion rare, germination precocious, few cells formed within spore wall, sometimes prior to dehiscence; germinated spores seen among leaves.

Type: CANADA. British Columbia: Vancouver Island, Strathcona Provincial Park, Forbidden Plateau, trail to summit of Mt. Becher, 49°39'N, 125°12'W, dry exposed rock outcrop, on rock, 12 August 1969, R. L. Halbert 4231 (holotype, UBC).

Additional specimens examined: CANADA. British Columbia: Vancouver Island, Strathcona Provincial Park, Donnes Mt., 49°42'N, 125°54'W, 19 August 1970, Halbert & Price 6507 (UBC). North Vancouver, Mt. Seymour, 9 October 1960, Schofield 12555 (UBC), Murray, 21 July 1980 (ALA). USA. California: Del Norte Co., above Whisky Lake, 41°55'N, 123°39'W, 25 November 1980, Norris 57721 (HSC). Siskiyou Co., 1 mi W of Elk Lick, 20 August 1972, Norris 23220 (HSC).

Distribution (Fig. IV-2) and Ecology. Andreaea schofieldiana is apparently very rare and is known only from the localities cited above in southwestern British Columbia and northernmost California.

Andreaea schofieldiana has been found between about 1280 and 1460 m elevation in British Columbia and 1525 and 1830 m in California. It grows on dry, exposed as well as moist, shaded acidic rock surfaces (including granite) on subalpine slopes of open conifers, such as mixed Tsuga mertensiana and Abies lasiocarpa in British Columbia and scattered Picea breweriana in California. One British Columbian collection was made in a subalpine cirque. Andreaea heinemannii Hampe & C. Müll. (= A. angustata Lindb. ex Limpr.) was associated with A. schofieldiana in one collection on a dry, exposed, south-facing rock in British Columbia.

Differentiation and Relationships. See Table IV-1. Its much smaller spores (Fig. IV-1: 2, 3) differentiate A. schofieldiana from both A. rothii ssp. rothii and A. megistospora ssp. megistospora (Fig. IV-3: 11-13), which occur in northwestern North America and like A. schofieldiana have leaves in which the lamina is distinct to the apex. Andreaea schofieldiana is apparently most closely related to the European endemic species, A. frigida Hüb., with which it shares medium-sized spores and lanceolate leaves in which the lamina is distinct to the apex. In A. schofieldiana, however, spores are smaller, the costa is more strongly biconvex, leaf texture is membranous rather than cartilaginous, a few low papillae occur occasionally on inner gametoecial bracts, and the habitat is drier. There is also a greater tendency toward fragile leaf tips, that in A. schofieldiana are sometimes swollen and notched as in Didymodon johansenii (Williams) Crum.

Andreaea schofieldiana has been mistaken for A. nivalis Hook. (as has A. frigida), no doubt because of the strong costa, lanceolate leaf, and sometimes similar bronze-green color. But closer inspection shows that A. schofieldiana has convolute perichaetial bracts and lacks the sharp leaf papillae of A. nivalis.

Etymology. Andreaea schofieldiana is named for Dr. W. B. Schofield, bryologist, plant geographer, professor of botany, and curator at the University of British Columbia. His numerous collections of Andreaea from British Columbia and elsewhere are of inestimable value for monographic study. His affection for the Andreaeopsida is manifest on the jacket of his superb bryology text (Schofield 1985).

Andreaea megistospora B. Murray, sp. nov.
ssp. megistospora (Fig. IV-3: 9-23, Fig. IV-4: 25-28)

Andreaea sect. Nerviae. Admodum parva; folia plus minusve subito contracta supra basem; lamina parte distali folii distincta; costa protuberans in pagine dorsali; perichaetii bracteae interiores papillosae. Haec species differt ab omnibus congeneribus sporis amplissimis, (40)50-90(110) um diametro.

Plants small, rarely medium-sized, densely tufted, black, brown-black, green-black, or brown; junvenile leaves and inflorescences red-brown; saxicolous. Protonemata typical of the genus. Rhizoids uni- and bi-seriate. Protonemal appendages rarely seen. Stems erect to curved, usually less than 1 cm high, rarely to 1.5 cm. Axillary hairs frequent, persistent, with brown mucilaginous cells. Primary leaves irregularly lanceolate to partly filamentous, sometimes partially bistratose, about 0.05-0.40 mm long. Juvenile leaves about 0.1-0.2 mm long, broadly ovate, apiculate. Mature leaves evenly spaced, when moist erect-spreading or secund, when dry appressed, apices slightly curved to secund; usually abruptly tapering from an ovate or oblong base, often sharply contracted at the shoulder to a subula that is 2 to 3 times as long as the leaf base; to 1.8(2) mm long, lamina in subula distinct, unistratose or partly to completely bistratose, base usually unistratose; apices acute to slightly rounded; bases clasping, slightly narrowed to the straight or slightly decurrent insertion; margins plane to slightly incurved, entire. Costa present, single, distinctly delimited, transition between lamina and costa distinct, dorsal (and sometimes ventral) costal surface bulging, especially between the shoulder and midleaf; narrow, about 1/6 the width of the leaf base (rarely weak basally in subperichaetial leaves), usually tapering above, percurrent to excurrent, sometimes filling upper 1/4 of limb; basal cells elongate, sinuose, cells in lower subula short-rectangular and often papillose, in upper subula round and similar to laminal cells; in transverse section of up to 6 layers of little differentiated thick-walled cells. Laminal cells mostly round to oblate, 7-10 µm long, 9-11 µm wide, evenly thin-walled, smooth, becoming somewhat longer in base, in subcostal region of leaf base often yellow, oval to rectangular with slightly pitted, frequently finely sinuose walls; basal marginal cells mostly rounded to quadrate, a few rectangular, especially in subperichaetial leaves. *Cladautoicous and gonioautoicous*. *Perigonia* narrowly gemmate, bracts about 0.8 mm long, inner convolute with low papillae; antheridia about 4-6, about 0.4 mm long, paraphyses numerous, partially biseriate apically. *Perichaetial bracts* differentiated, ovate-oblong, convolute and sheathing, about 2 mm long, basal cells often sinuose; inner bracts ecostate, unistratose or with small bistratose patches, papillose, papillae usually low and rounded, rarely sharp and oblique, outer bracts costate, apiculate, usually epapillose; archegonia lateral or terminal, 3-4 produced sheathed in one ecostate slightly inrolled bract. *Sporophytes* common, mature in summer, overwintering as immature capsules within perichaetia, brown spores seen in immature capsules in April and early November collections from Scotland; in British Columbia capsules almost mature in April, dehisced in June, premeiotic capsules seen in July. Capsules shortly exserted on pseudopodia; pseudopodia usually single (bipseudopodiate plants seen rarely); capsules about 0.7-0.8 mm long, base of capsule below valves usually occupying about 1/3 the length of the capsule. *Calyptrae* typical of the genus. *Spores* angled to round, brown, very large (40)50-90(110) μm, very finely papillose to striate-reticulate-papillose; spore abortion rare, germination precocious, numerous cells formed within spore wall, sometimes prior to dehiscence; numerous multicellular spores with germ tubes and rhizoids seen among stems and leaves.

Type: UK. Scotland: Main Argyll (vice-county 98), Meeting of Three Waters, Pass of Glencoe, national grid reference 27/17.56, on exposed surfaces of granite boulders, 31 October 1982, *B. M. Murray & D. G. Long s.n.* (*holotype*, E; *isotypes*, ALA and others to be distributed in an exsiccata of *Andreaea* in preparation).

Additional specimens examined: I have examined pertinent material in ALA, BBSUK, BM, DBN, E, NMW, O, TRH, UBC, and WTU and have identified approximately 145 collections. The 90 or so collections from British Columbia (most in UBC) and 35 odd from the British Isles are abstracted below. Less numerous collections from the United States (9) and Norway (12) are cited more completely. Numbers in parentheses represent the number of collections seen from an area; an asterisk (*) represents a specimen lacking spores, identified by leaf characters. USA. Alaska: Baranof I., E edge of Davidof L., 56°37'N, 134°50'W, *Worley & Hamilton 9821* (UBC); Sitka, below Blue L., 57°04'N, 135°10W, *Worley & Hamilton 9215* p.p. (UBC). Prince of Wales I., Nichols Bay, 54°41'N, 132°05'W, *Frye*, 6 August 1913 (NY, S p.p.). Washington: Snohomish Co., Granite Falls, *Bailey*, 21 March 1925 (WTU), Perry Creek Falls trail, *Hermann 18495* (COLO), *Ireland 7815* (DUKE), *Schofield & Ireland 21731* (UBC); Big Four, near Silverton, *Schofield & Williams 26058* (UBC). CANADA. British Columbia: Queen Charlotte Islands: Graham I. (8), Moresby I. (22), Kunghit I. (4), Chaatl I. (3); Prince Rupert area: Skeena R. (1); Pitt I. (6), Bonilla I. (1), Estevan Group, Dewdney I. (1), Moore I. (1), Calvert I. (4), Quadra I. (2); north of Vancouver: Shannon Falls (6), Mt. Seymour (2); Vancouver Island: Brooks Peninsula (9), Tahsish Inlet area (5), Effingham Inlet (3), Kennedy L. (4), Mt. Arrowsmith (3), Mt. Benson (1); Eagle Summit (1); Haney

Research Forest (1); Indian Arm (1); Stave L. (1). NORWAY. Möre: Romsdal amt., Hustal i Bod, *Kaalaas*, 3 August 1907 (0). Hordaland: Sund: Telavag, *Størmer*, 24 June 1950 (0*); Eide, *Størmer*, 4 May 1965 (0). Rogaland: Eigersund, *Størmer*, 5 June 1951, 27 July 1972, 31 July 1972 (0*). Bjerkreim, *Størmer*, 8 June 1951, 28 July 1972 (0). Sokndal, *Størmer*, 13 June 1951 (0). Stavanger amt., Vindafjord, Skjold Hval, *Hagen*, 23 July 1912 (TRH); Lyse, *Hagen*, 13 August 1912 (0); Frisdalen ved Bergen, *Wulfberg*, 27 August 187? [year illegible] (0). BRITISH ISLES. Scotland: Outer Hebrides, Harris (1, BM*); West Sutherland (1, UBC); West Ross (2, E); North Ebudes, Skye (2; ALA, E, NMW*); Easterness (1, NMW); Westerness (5; ALA, BM, E, NMW, UBC); Mid Perthshire (1, BM), West Perthshire (1, DBN*); Main Argyll (6; ALA, BM, E, NMW, UBC); Dunbartonshire (1, E); Clyde Isles, Arran (1, E*); Peebleshire (1, BBSUK*); Wigtownshire (1, BBSUK); Kirkudbrightshire (1, BBSUK). England: Cumberland (1, BM); County Durham (1, BM). Wales: Merioneth (3; BBSUK, NY); Pembrokeshire (1, ALA*). Ireland: Mid-Cork (1, BM); West Cork (1, DBN*); Down (1, DBN).

Distribution (Fig. IV-5) *and Ecology*. *Andreaea megistospora* ssp. *megistospora* is known only from the localities cited above. Like the recently described *A. sinuosa* B. Murr., ssp. *megistospora* belongs to the group of western North American-western European disjuncts that occur in oceanic regions and are considered relicts whose ranges were sharply contracted during climatic and vegetational change during the Quaternary (Murray 1986).

A. megistospora (including ssp. *epapillosa*, described below) is quite common in western North America. Almost all material previously identified as *A. rothii* has turned out to be *A. megistospora*. From western North America I have seen about 110 collections of *A. megistospora* and only about 15 of *A. rothii*. In northwestern Europe, however, *A. rothii* is by far the more common species. For example, from the British Isles, I have seen about 35 collections of ssp. *megistospora* and about 775 of *A. rothii*.

Andreaea megistospora occurs on acidic rock from near sea-level to subalpine elevations in regions with a cool, hyperoceanic climate. It has been found at elevations from near 0 to 610 m in North America and from 10 to 700 m (one collection from 1100 m) in Scotland. The known latitudinal range is about 48-57°N in North America and 52-63°N in Europe.

About one-third of the collections had label data about exposure or moisture. Of these almost 95 per cent reportedly grew on dry, open, sunny or exposed rock surfaces (granite, granodiorite, quartzite, and sandstone). The remaining five per cent were from moist to wet surfaces. Schofield (1976) described the British Columbian habitat of *A. rothii* (almost all collections have been redetermined as *A. megistospora*) as "on dryish acidic rock from near sea-level to subalpine elevations, normally in exposed sites that dry out rapidly." My field experience with ssp. *megistospora* is mostly in Scotland where it occurs on dry, moist or wet, usually exposed rock. It can be associated with *A. rupestris* Hedw. var. *rupestris*, *A. rothii* ssp. *falcata* (Schimp.) Lindb. (= *A. huntii* Limpr.), and *A. alpina* Hedw., all or which are widely distributed in the British Isles, more rarely with *A. mutabilis* Hook. f. & Wils.

Differentiation. See Table IV-1. The very large spores of Andreaea megistospora, (40)50-90(110) μm (Fig. IV-3: 11-13), the largest in the genus (and the reason for the epithet), differentiate it from its congeners. Most spores of A. rothii, its closest relative, are between 35 and 50 μm.

When mature capsules are not present, spore size can sometimes be determined even in young capsules, since, in Andreaea, spores form, turn brown, and reach mature size early in capsule development. Also old spores are often seen in the bases of otherwise disintegrated old capsules or among old perichaetial bracts.

If spores are not present, however, regular occurrence of papillae on perichaetial bracts distinguishes ssp. megistospora from A. rothii ssp. rothii, A. frigida, and A. schofieldiana. The lamina is distinct to or to near the leaf apex in ssp. megistospora, whereas in A. rothii ssp. falcata the lamina is narrower and less distinct, and the costa often fills much of the subula. Subspecies megistospora is distinguished from ssp. epapillosa by the presence of papillae on perichaetial bracts, the lamina which remains distinct in the limb, the costa sometimes filling just the uppermost limb, and the transition between lamina and costa distinct with the costa bulging dorsally (Fig. IV-4: 25-28).

Andreaea megistospora B. Murray ssp. epapillosa B. Murray, ssp. nov.
(Fig. IV-3: 24, Fig. IV-4: 29-32)

Haec subspecies differt a ssp. megistospora lamina subulae indistincta, costa excurrenti subulam distalem complenti nullo modo protuberanti in pagina dorsali, bracteis perichaetialibus epapillosis.

A plant with many of the features of ssp. megistospora. It is separated on account of leaves with the lamina indistinct in the subula, the subula three to four times as long as the leaf base, the costa usually 4-layered, frequently filling the upper half to two-thirds of the subula, the transition between the lamina and costa indistinct (dorsal costal surface not bulging), and the epapillose perichaetial bracts.

Type: CANADA. British Columbia: Queen Charlotte Islands: W. Moresby I., Sunday Inlet, 52°38'N, 131°55'W, cove on north side, outcrops in bog, 11 July 1966, W. B. Schofield 31437 (holotype UBC).

Additional specimens examined: USA. Alaska: Baranov I., Sitka, below Blue L., 57°04'N, 135°10'W, Worley & Hamilton 9215 p.p. (UBC); between Blue L. and Silver Bay, 57°03'N, 135°11'W, Worley & Hamilton 9413 (UBC). Price of Wales I., Nichols Bay, 54°41'N, 132°05'W, Frye, 6 August 1913 p.p. (S). CANADA. British Columbia: Queen Charlotte Islands: Graham I., Van Inlet, 53°15'N, 132°33'W, Schofield 33612 (UBC); Moresby I., Schofield 24046 p.p., 25324, 30790, 31187, 31231, 31390 p.p., 37386, 73490 p.p. (UBC); Chaatl I., Schofield & Boas 18786 p.p., 18862 (UBC). Vancouver Island: Brooks Peninsula, Schofield 68565, 82550 (UBC); Nasprti Inlet, Halbert 7805 (UBC).

Distribution (Fig. IV-6) and Ecology. *Andreaea megistospora* ssp. *epapillosa* is known only from hyperoceanic islands of southeastern Alaska and British Columbia between about 50° and 57°N. Its ecology is apparently similar to that of ssp. *megistospora*; about half of the collections were mixtures of the two subspecies.

Differentiation. Subspecies *epapillosa* (Fig. IV-4: 29-32) is separated from ssp. *megistospora* (Fig. IV-4: 25-28) by its epapillose perichaetial bracts (the reason for the epithet), the lamina that is indistinct in the often longer subula, and the costa that is excurrent and fills most of the subula and does not bulge on its dorsal surface. If spores are present it is easily distinguished from *A. rothii*; if not it is distinct from most specimens of ssp. *rothii* by its excurrent costa filling the subula and from ssp. *falcata* by its epapillose perichaetial bracts. *Andreaea heinemannii* (= *A. angustata*) is another species with the costa often filling the subula that occurs in western North America. It is usually seen with sporophytes and can be distinguished from ssp. *epapillosa* by its much smaller spores, less than 40 µm. It also differs by usually having rectangular basal marginal cells.

The following key includes major differences between the taxa described here and other costate *Andreaeae* in North America and Europe. I have emphasized spore size since it is the most reliable feature and since leaf characters often have variable states within a taxon. Sporophytes are usually present, and even if they are not at the mature stage, spores can usually be found among leaves or in decayed capsule bases. If spores are absent, taxa can be identified by scanning the key for subsidiary features or by reference to Table IV-1.

Key to Costate *Andreaeae* of North America (North of Mexico) and Europe

1. Leaf margins crenate to serrate throughout, with sharp laminal and costal papillae. Perichaetial bracts shaped like stem leaves. Subgenus *Chasmocalyx* (Braithw.) Lindb. .... *A. nivalis*

1. Leaf margins entire or very rarely dentate above, laminal papillae absent on mature leaves, low costal papillae often present. Perichaetial bracts differentiated, convolute. Subgenus *Andreaea* sect. *Nerviae* 2

2. Spores 11-19(23) um. Basal laminal cells mostly rectangular, walls little pitted, not sinuose. Dioicous ... *A. blyttii* Schimp.

2. Spores larger than 20 um. Basal laminal cells mostly quadrate, round, to oblate, sometimes rectangular near costa or margins, walls often pitted and sinuose. Autoicous 3

3. Most spores smaller than 35 um 4

3. Most spores larger than 35 um 7

4. Costa weak, at most 4-layered above and often lacking basally. Usually with a few rectangular basal marginal cells ....
.... *A. heinemannii*

4. Costa usually strong throughout, often 5-6-layered above. Basal marginal cells mostly quadrate or rounded, very rarely one or two short-rectangular 5

5. Lamina indistinct in upper part of leaf, costa often filling subula. Transition between lamina and costa indistinct (dorsal costal surface not bulging). Leaves ± abruptly contracted at shoulder, forming a subula .... *A*. *crassinervia* Bruch

5. Lamina distinct to leaf apex, costa occasionally filling upper part of limb. Transition between lamina and costa ± distinct. Leaves lanceolate or gradually tapering from shoulder 6

6. Spores (20-24)28-36(40-50) um. Endemic to Europe ..... *A*. *frigida*

6. Spores 20-30(36) um. Endemic to western North America .... *A*. *schofieldiana*

7. Spores (30)35-50(rarely over 60, to 80) um 8

7. Spores (40)50-90(110) um 9

8. Inner perichaetial bracts epapillose. Lamina usually distinct to near apex, costa sometimes filling uppermost part of limb. Leaves usually weakly falcate, rarely brittle; margins entire or with strongly bulging marginal cells .... *A*. *rothii* ssp. *rothii*

8. Inner perichaetial bracts papillose above. Costa usually filling upper subula or rarely lamina distinct to near apex. Leaves usually strongly falcate and brittle; margins entire or rarely distantly dentate above .... *A*. *rothii* ssp. *falcata*

9. Lamina distinct to leaf apex, costa occasionally filling upper part of limb. Transition between lamina and costa distinct (dorsal costal surface bulging). Inner perichaetial bracts papillose above .... *A*. *megistospora* ssp. *megistospora*

9. Lamina indistinct in subula, costa filling most of subula. Transition between lamina and costa indistinct (dorsal costal

surface not bulging). Inner perichaetial bracts epapillose ......
.... *A. megistospora* ssp. *epapillosa*

Taxonomic Criteria of Sect. *Nerviae* and Realignment of Taxa Closely Related to *A. schofieldiana* and *A. megistospora*

Selection of spore size as the major defining character for sect. *Nerviae* has led to a different arrangement of taxa from that of Schultze-Motel (1970). Taxa in this section have long been misunderstood and many specimens have been misidentified. It seems to me this is because less stable leaf characters have been used and spore characters largely ignored.

In my view, sect. *Nerviae* consists of eight species, all but one found in the Northern Hemisphere. Because I have not sufficiently studied the single Southern Hemisphere species, *A. subulata* Harv. (Schultze-Motel 1970), it is not treated here. The relationship between *A. blyttii* and *A. heinemannii* (= *A. angustata*) will be discussed in another paper. The remaining five species, including the two described here, have been included within either *A. rothii* or *A. crassinervia* by Schultze-Motel (1970).

Schultze-Motel (1970) treated those Northern Hemisphere members of sect. *Nerviae* that have isodiametric basal marginal leaf cells as *A. rothii*, if the lamina extends to the leaf apex, and as *A. crassinervia*, if the costa completely fills the leaf apex. *Andreaea rothii* was divided into two subspecies: ssp. *rothii*, with the leaf quite abruptly narrowed to a subula from an ovate base, and ssp. *frigida* (Hüb.) Schultze-Mot., with the leaf gradually narrowed above the base.

Schultze-Motel also divided A. crassinervia into two subspecies: ssp. crassinervia, with the inner perichaetial bracts epapillose or with scattered low papillae, and ssp. huntii (Limpr.) Amann, in which inner bracts have high papillae. Spore size was not used as a diagnostic character, but, in descriptions of taxa, range of spore size in A. rothii ssp. rothii was given as 30-40 µm and that in ssp. frigida as 3[illegible]35 µm. Range of spore size for A. crassinervia ssp. crassinervia was given as 28-32 µm and for ssp. huntii as 32-40 µm, with spores as large as 48 µm reported in the literature.

I have found that the leaf characters traditionally used either have variable expressions within taxa or the various states occur repeatedly in unrelated Andreaeae. For example, all members of sect. Nerviae have at least some forms in which the costa fills the upper limb. And perichaetial bracts with variable degrees of papillosity are present in several taxa. I have also found that most size ranges of spores given in the literature are inaccurate (e.g. Khanna 1965, Schultze-Motel 1970). In fact, taxa sort out nicely by spore size classes.

Table IV-1 gives a synopsis of the distribution of the important diagnostic features of the taxa described here and of taxa treated by Schultze-Motel as A. rothii and A. crassinervia. If Schultze-Motel's scheme were followed, the taxa described here would be arranged very differently from the way I have presented them. Andreaea schofieldiana, A. frigida, A. rothii ssp. rothii, and A. megistospora ssp. megistospora all have leaves most like Schultze-Motel's rothii-type and would be lumped. But when spore size is taken into account, all these are seen to be distinct from each other. The taxa with similar leaf features are, in some cases, most closely related by spore size to taxa with very different leaf forms. Andreaea crassinervia and A. megistospora ssp. epapillosa have crassinervia-type leaves (sensu Schultze-Motel 1970), but they differ in other characters including spore size. The taxon that was treated by Schultze-Motel (1970) as A. crassinervia ssp. huntii is instead related to A. rothii by both spore size and leaf characters. It is synonymous with A. rothii ssp. falcata, which was treated as a nomen confusum by Schultze-Motel. The history of the confusion and status of this taxon is discussed in the revision of Andreaea in the British Isles (Chapter VI).

I am not sure why spores have been largely ignored by students of Andreaea. Perhaps it is because capsule characters are not very important in delineating taxa, and, by extension, it may have been assumed that this applied to spores also. Why, with rare exceptions (e.g. Nyholm 1969), sizes and size ranges have been inaccurately reported is also not clear. I have found that larger spores, over about 35 µm, tend to swell for some time after micro-preparations are made. For this reason, I have mounted all preparations in Hoyer's medium and have waited to measure spores until the solution dries. But the swelling of spores does not account for the discrepancies in reports.

The large range of spore size that occurs in taxa of the Andreaeopsida can result from two features of spore development. One is spore abortion, which occurs in most Andreaea species and often involves a large part of the spore mass. This results in two size ranges: one for brown, shriveled spores and the other for green, turgid spores. Spore abortion is rare in sect. Nerviae, however. The second factor is the universal occurrence of precocious germination. In the Andreaeopsida, multicellular masses form within the spore wall often prior to dehiscence. To accommodate the increase in diameter, the spore wall stretches and the ornamentation appears striate or reticulate as cracks occur in the outer layer. Spores in varying stages, with varying numbers of cells, occur in the spore mass, and the result is a wide size range. For example in *A. rothii*, spores within a capsule can range from 30 to 60 or so μm.

Based on spore size and on other features mentioned, it is clear that *A. schofieldiana* and *A. megistospora* are amply distinct from previously known *Andreaea* species. The western North American endemic species *A. schofieldiana* is most closely related to the European endemic, *A. frigida*. Because they have medium-sized spores, these two species appear to be more closely related to *A. crassinervia* than to *A. rothii*. Large-spored species, *A. rothii* and *A. megistospora* appear to be closely related, and large-spored stock could have diversified in the lowland to subalpine habitats in which these taxa are usually found. Subspecific rank, rather than specific, was chosen for *A. megistospora* ssp. *megistospora* and ssp *epapillosa* and for *A. rothii* ssp. *rothii* and ssp. *falcata* because the morphological leaf characteristics that define each of the taxa are of uncertain value. Since these features have variable states that recur throughout the genus *Andreaea*, I do not give them much weight. By utilizing subspecific rank, I emphasize the stable feature that unites the two species--spore size--in spite of how different their leaves may appear.

Acknowledgements

I am grateful especially to D. G. Long (E), A. R. Perry (NMW and BBSUK), and W. B. Schofield (UBC) for guidance in the field, hospitality, help with mapping, and access to and loan of specimens; to curators and staff of the following herbaria for access to or loan of specimens: BBSUK, BM, COLO, DBN, DUKE, E, HSC, NMW, NY, O, S, TRH, UBC; and to O. I Rønning for help in mapping Norwegian localities. Kay W. Holmes did the drawings. D. F. Murray criticized the manuscript. Field work in Scotland was supported by the University of Alaska Museum.

Table IV-1. Comparison of *Andreaea schofieldiana*, *A. megistospora* and their closest relatives

	schofieldiana	*frigida*	*crassinervia*	*rothii*		*megistospora*	
				ssp. *rothii*	ssp. *falcata*	ssp. *megistospora*	ssp. *epapillosa*
Spore size	mid-sized, 20-30(35) µm	mid-sized, (20)25-35 (40) µm	mid-sized, (20)26-36 (40-50) µm	large, (30)36-52(60-80) µm		very large, (40)50-90(110) µm	
Leaf taper	lanceolate or limb gradually formed	lanceolate or limb gradually formed	limb ± abruptly formed	limb ± abruptly formed		limb ± abruptly formed	
Lamina in upper part of leaf	distinct	distinct	indistinct	distinct	indistinct to distinct	distinct	indistinct
Costa	percurrent to excurrent and filling uppermost part of leaf	percurrent to excurrent and filling uppermost part of leaf	excurrent, almost completely filling subula	percurrent to excurrent and filling uppermost part of leaf	excurrent, usually filling upper subula, rarely percurrent	percurrent to excurrent and filling uppermost part of leaf	excurrent, almost completely filling subula
Transition between lamina and costa above shoulder	distinct, costa strongly biconvex	± distinct, costa biconvex or bulging dorsally	indistinct, costa not bulging dorsally	± distinct, costa bulging dorsally		distinct, costa biconvex to bulging dorsally	indistinct, costa not bulging dorsally
Perichaetial bract ornamentation	papillae occasional, low and scattered	papillae absent	papillae present, usually scattered, or absent	papillae absent, rarely very low and scattered	papillae present, high and dense, rarely lacking in some plants within a population	papillae present, low to rarely high	papillae absent
Ecology	subalpine; dry to moist	alpine; wet	alpine; wet	predominately lowland, reaching low alpine; dry to occasionally wet		predominately lowland, reaching low alpine; dry to occasionally wet	
Distribution	northwestern North America	Europe	Europe and eastern North America	Europe and North America (reported from Mongolia)	Europe and one collection seen from Oregon	northwestern Europe and northwestern North America	northwestern North America

Figure IV-1. Illustrations of Andreaea schofieldiana. Drawn from holotype (Halbert 4231, UBC) unless noted. -- 1. Habit, leaves moist. -- 2. Spores. -- 3. Germinated spores. -- 4. Transverse sections of upper part of leaves, (unistratose section from Murray, 21 July 1980, UBC). -- 5. Mature leaves. -- 6. Juvenile leaf. -- 7. Primary leaf and axillary hairs.

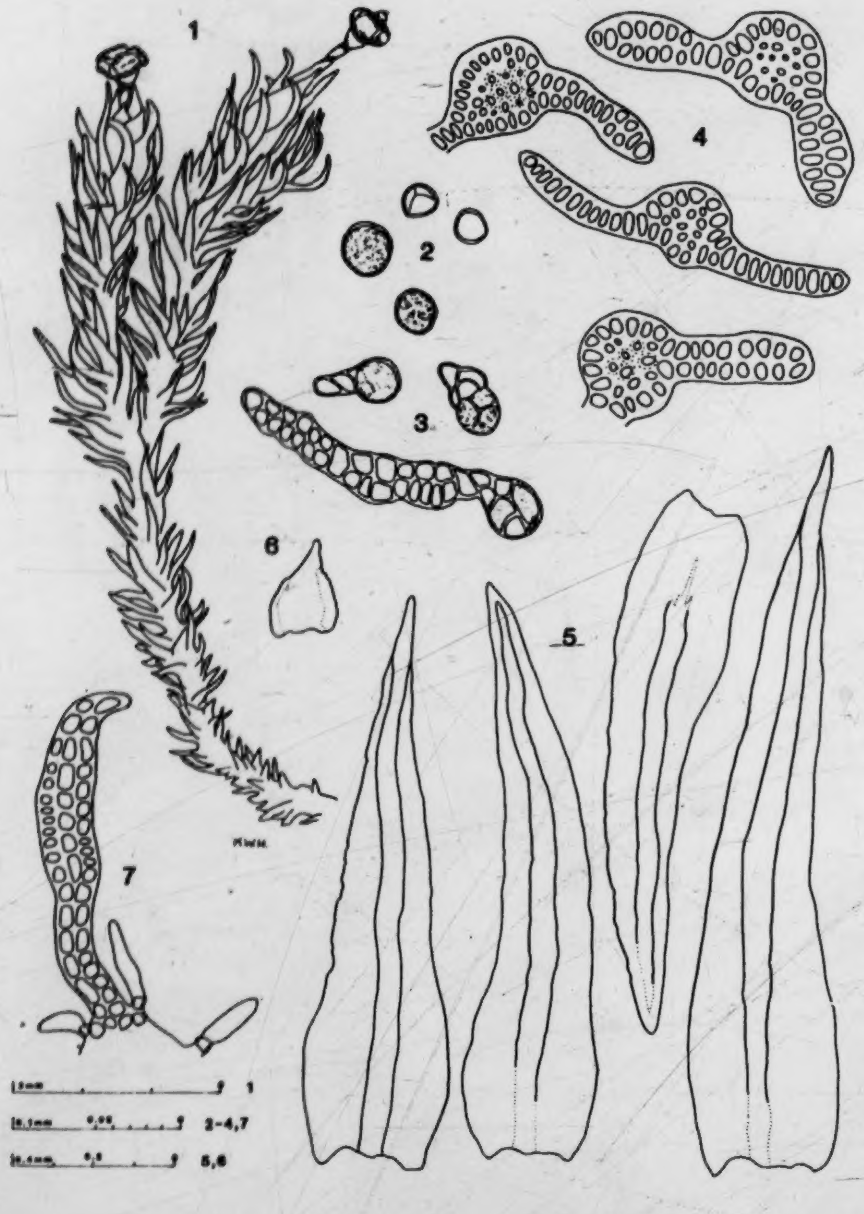

KWH
1mm 0 1
0,1mm 0,05 0 2-4,7
0,4mm 0,2 0 5,6

Figure IV-2. Distribution of Andreaea schofieldiana.

WORLD, NORTHERN HEMISPHERE

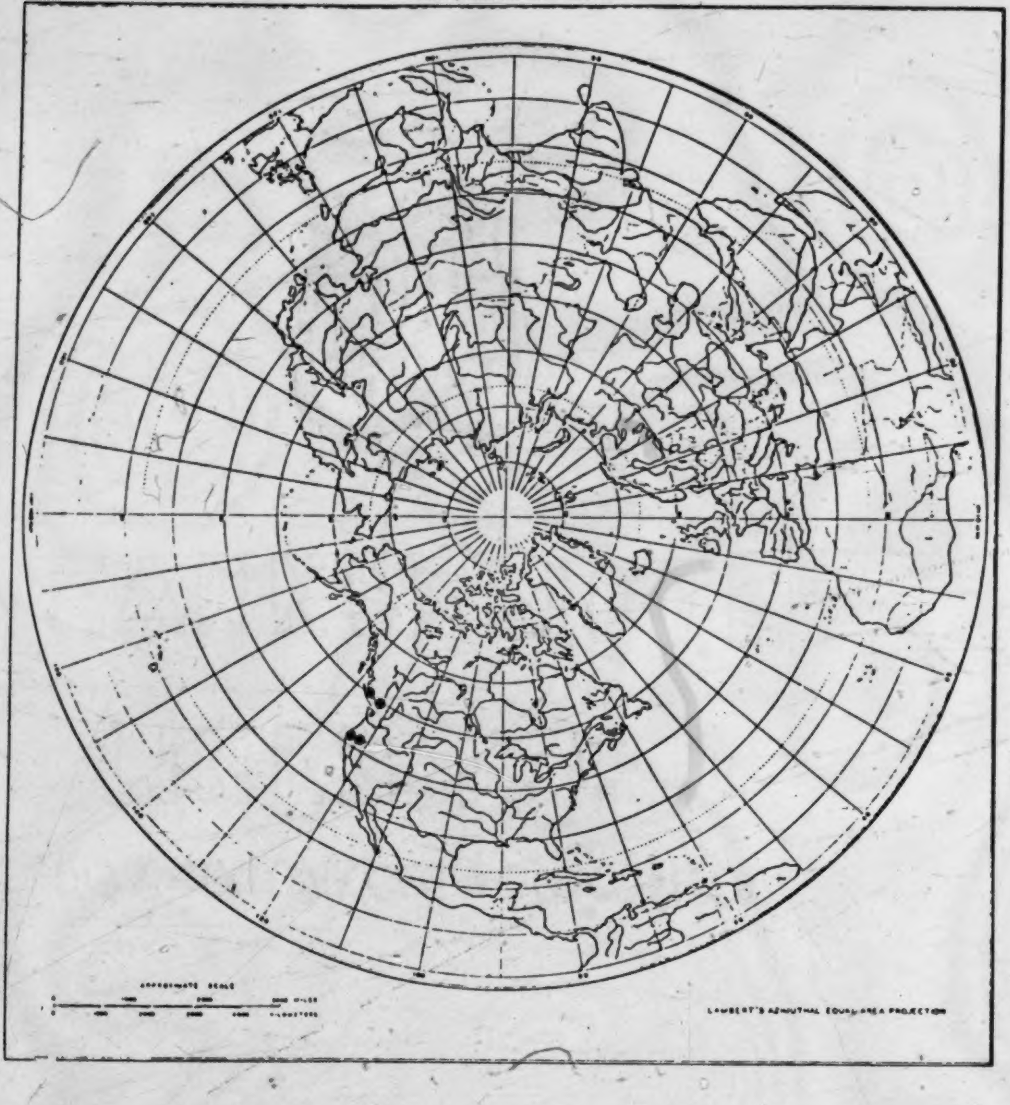

APPROXIMATE SCALE
MILES
KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

Figure IV-3. Illustrations of *Andreaea megistospora*. -- 9-23. Ssp. *megistospora*. Drawn from holotype (31 October 1982, *Murray & Long s.n.*, E) unless noted. -- 9. Habit, leaves moist (from *Schofield 24985*, UBC). -- 10. Habit, leaves moist, with perichaetium. -- 11. Tetrads, upper from very young, green capsule, spores hyaline (from *Schofield 43476*, UBC); lower from immature capsule, spores yellow. -- 12. Spore. 13. Germinated spore (from *Halbert 7594*, UBC). -- 14. Primary leaf (from *Halbert 3695*, UBC). -- 15. Primary leaves (from *Murray & Perry*, 1 August 1984, ALA). -- 16. Transverse section of stem. -- 17. Axillary hair. -- 18-20. Cells from upper, middle and lower parts of leaf. -- 21. Mature leaves. -- 22. Juvenile leaves. -- 23. Outline of primary leaf (Fig. 14) at branch bud. -- 24. Ssp. *epapillosa*. Germinated spore (from *Schofield 25324*, UBC).

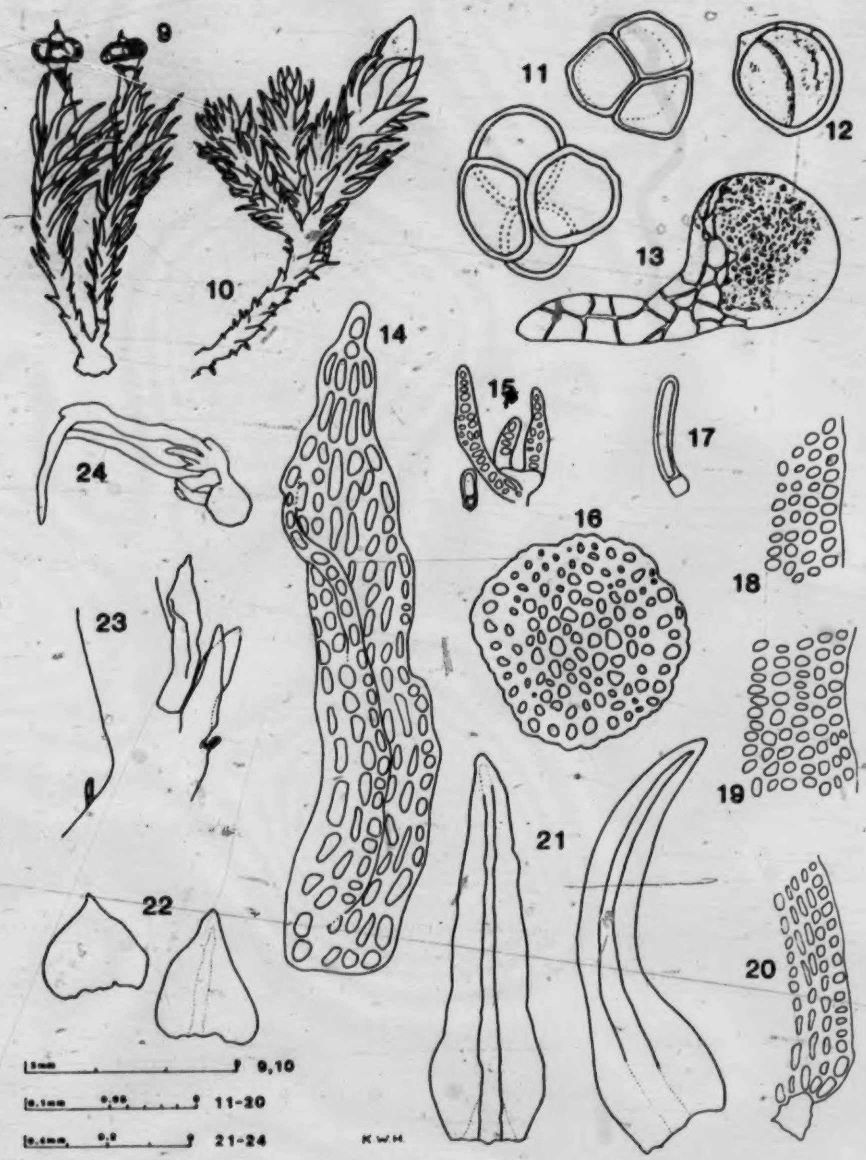

9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
3mm
9,10
0,1mm
0,05
11-20
0,4mm
0,2
21-24
KWH

Figure IV-4. Illustrations of *Andreaea megistospora*. -- 25-28. Ssp. *megistospora*. Drawn from holotype (31 October 1982, *Murray & Long s.n.*, E) unless noted. -- 25. Mature leaves (one on right from *Murray & Perry*, 1 August 1984, ALA). -- 26. Transverse sections above mid-leaf. -- 27. Papillose cells of inner perichaetial bract, side view on left, surface view on right. -- 28. Transverse section of papillose cells of perichaetial bract. 29-32. Ssp. *epapillosa*. Drawn from holotype (*Schofield 31437*, UBC) unless noted. -- 29. Mature leaves (from *Schofield 25324*, UBC). -- 30. Transverse sections above mid-leaf (from *Schofield 31390*, UBC). -- 31. Epapillose cells of inner perichaetial bract, side view on left, surface view on right. -- 32. Transverse section of epapillose cells of perichaetial bract.

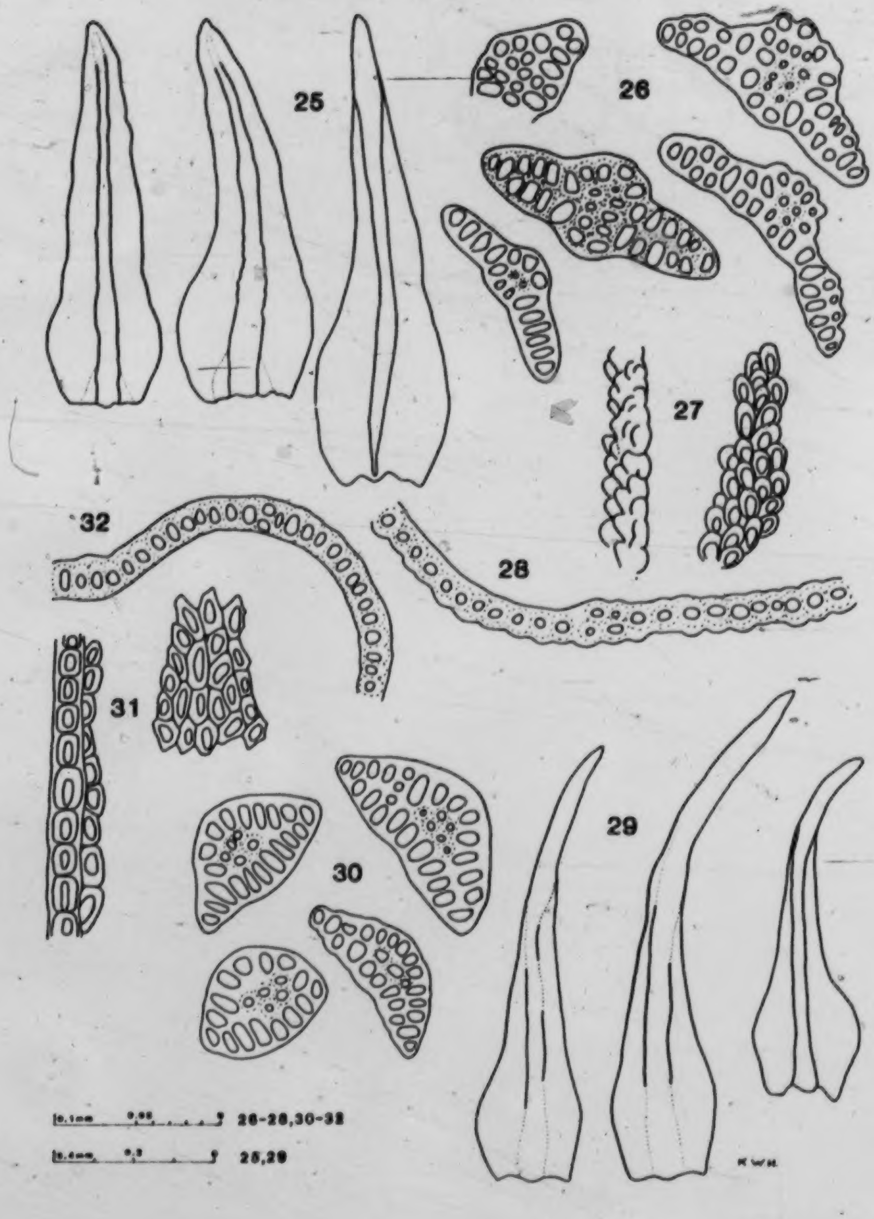
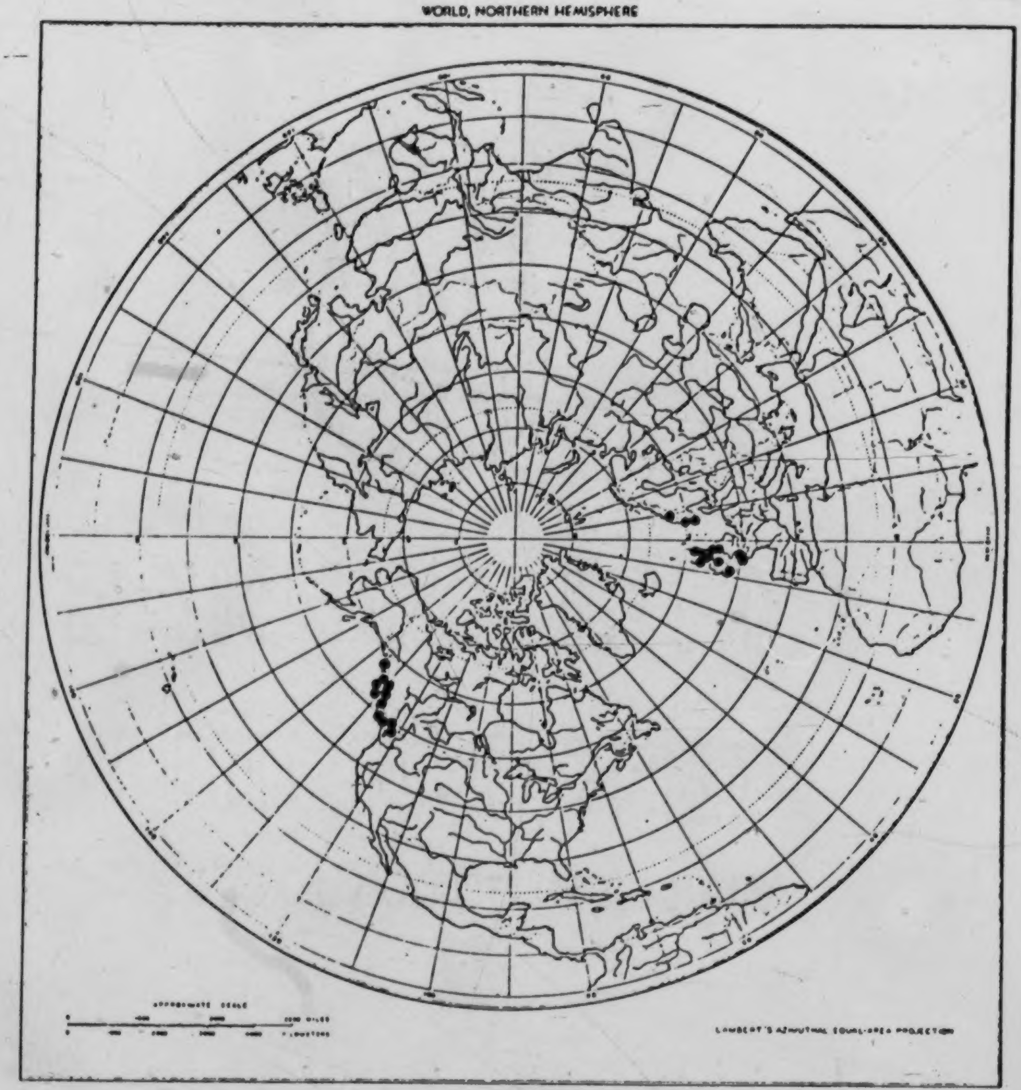

25
26
27
28
32
31
30
29
0.1mm 0.05 0
26-28,30-32
0.4mm 0.2 0
25,29
KWH

Figure IV-5. Distribution of *Andreaea megistospora* ssp. *megistospora*.

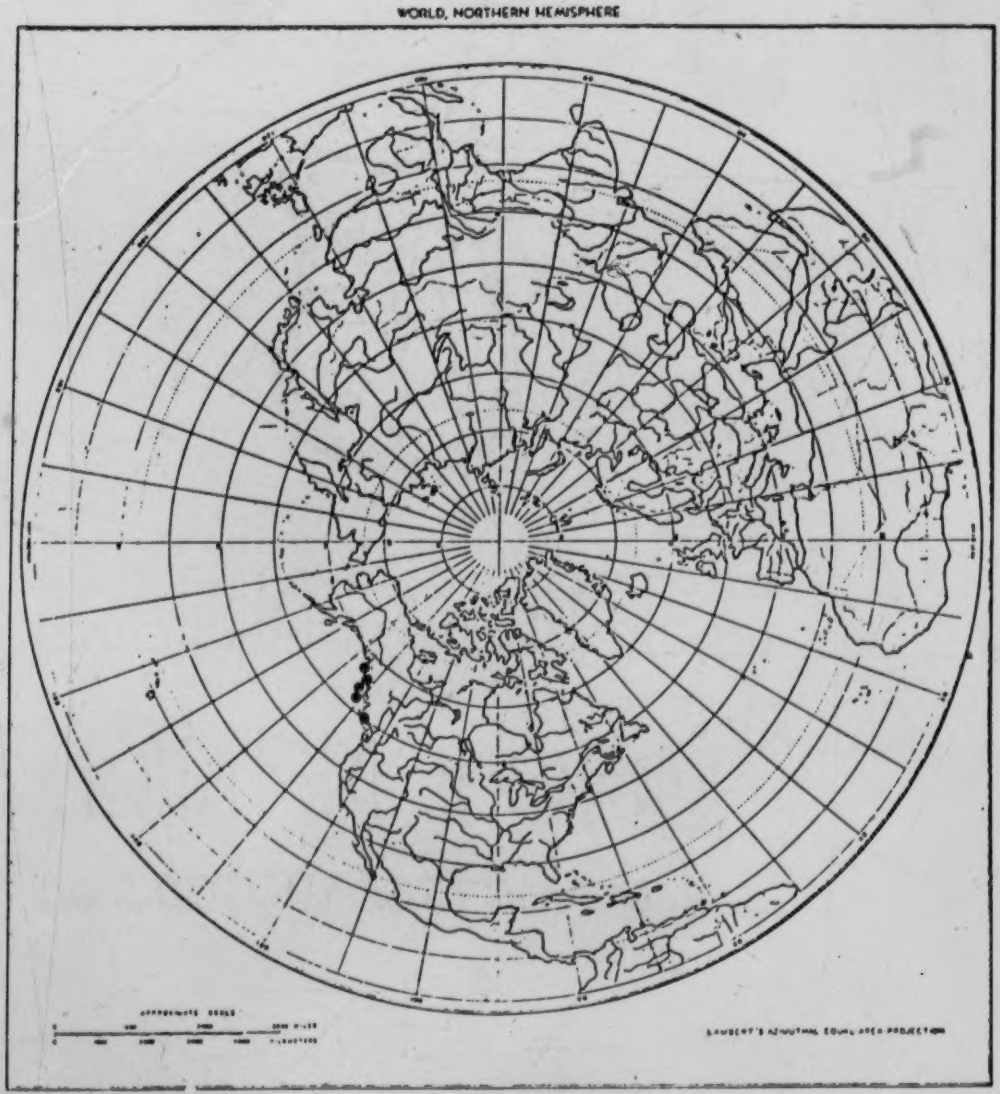


WORLD, NORTHERN HEMISPHERE

APPROXIMATE SCALE
2000 MILES
KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

Figure IV-6. Distribution of _Andreaea megistospora_ ssp. _epapillosa_.

WORLD, NORTHERN HEMISPHERE


APPROXIMATE SCALE
MILES
KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION

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Nyholm, E. 1969. Illustrated Moss Flora of Fennoscandia II. Musci. Fascicle 6: 688-696. Swedish Natural Science Research Council, Stockholm.

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V. ANDREAEOPSIDA OF ARCTIC NORTH AMERICA AND GREENLAND[1]

Andreaeobryaceae

A family with one genus and one species that is related to the Andreaeaceae primarily by dehiscence of the capsule by means of longitudinal valves and the massive sporeling that germinates within the spore wall and produces thallose protonematal appendages. In addition, stomata are absent from both families. The major differences between the two families are expressed in the following key:

1. Capsules elevated prior to maturity on short, stout setae, pseudopodia absent; capsules little changed in shape wet or dry, turbinate, obtuse-conic above, bases abruptly contracted to setae. Sutures consisting of thin-walled cells absent, valves apparently formed by breaks in thick-walled exothecial cells at areas of weakness. Exothecial cells of valves quadrate to short-rectangular; in transverse section triangular, inner walls at base of triangle very thin, other walls very thick. Calyptrae large, covering entire capsule, often persisting to maturity. Leaves costate. Axillary hairs with hyaline to partly brownish, rounded-rectangular basal cells, with beaked terminal cells; mucilage apparently extruded apically. On calcareous rock .... Andreaeobryaceae

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[1] A version of this chapter has been accepted for publication. Murray, B. M. 1986. Meddr. Grønland, Biosci. 23: 1-36.

1. Capsules elevated at maturity on pseudopodia, setae absent; capsules contracted and valves bulging when dry, lengthened and elliptic and valves closed when wet. Sutures consisting of thin-walled cells present. Exothecial cells of valves long-rectangular; in transverse section usually oval, all walls incrassate. Calyptrae small, apical, often falling early. Leaves costate or ecostate. Axillary hairs with brown, quadrate basal cells, with clavate to cylindrical upper cells; mucilage apparently extruded through numerous breaks in walls of upper cells. On acidic or basic rock or soil .... Andreaeaceae

1. Andreaeobryum Steere & B. Murr., Phytologia 33: 407. 1976. - Type: A. macrosporum Steere & B. Murr.

With features of A. macrosporum.

1. Andreaeobryum macrosporum Steere & B. Murr.

Phytologia 33: 407. 1976. - Type: Alaska. Brooks Range, Lake Peters, 69°20'N, 145°00'W; 1974 Murray 6713; holotype in NY, isotypes in ALA and 13 others, seen.

Plants medium-sized to very large and robust, caespitose, perennial, black to dark brown, green only when young or shaded, often with whitish calcareous incrustation below. Massive, globose, multicellular protonemata formed within stretched spore wall, from which branched thallose protonemata, rhizoids and persistent, cylindrical, multiseriate protonematal appendages up to 2 mm long are produced. Stems 2--4 (6 or more) cm long, irregularly branched, often by innovations, in transverse section of ± uniform thick-walled cells, cortical cells sometimes smaller and thicker walled than inner cells, central strands absent. Rhizoids basal on stems and sometimes branches, filamentous, uniseriate, red-brown. Minute, imbricate scale-like leaves occur frequently along lower portions of stems, on flagelliform shoots or in areas on middle portions of stems. Irregularly shaped primary leaves resembling pseudoparaphyllia can occur at bases of 6 stems and branches. Leaves spirally arranged, larger and denser at stem apices, sometimes eroded along lower portions of stems; leaves falcate-secund, narrowly lanceolate, tapering from broad bases to thick, narrowly obtuse subulae, 1.0--1.7 mm long, 0.2--0.25 mm wide near the base. Costae present, single, strong, indistinctly delineated, broad, up to 1/4 or 1/3 the width of leaf bases, decurrent, filling upper subulae, in transverse section of ± uniform, thick-walled cells. Laminae decurrent, unistratose at extreme bases, becoming bistratose above. Laminal cells rounded--quadrate to short-rectangular, thick-walled, not pitted, not collenchymatous; 12--14 µm wide, bulging, without or with very low papillae; alar cells not differentiated. Margins plane, entire or crenate due to convexity of laminal cells. Axillary hairs consist of 1(2 or more) hyaline to partly brownish, mostly short-rectangular, basal cells and elongate terminal cells that are abruptly and broadly rounded above and possess a terminal beak, similar to those of the moss-like hepatic genus *Takakia*; similar hairs produced on rhizoids and protonemata of mature plants and sporelings. Dioicous. Gynoecial paraphyses not seen. Perichaetial leaves little differentiated from stem leaves, not sheathing or convolute, margins crenate; innermost leaves minute. Archegonia terminal or lateral, usually 1--4. Androecia terminal or lateral, bulbiform, leaves concave, innermost ecostate, margins crenate, paraphyses numerous; antheridia usually 4--6, elliptic, on biseriate stalks. Pseudopodia absent.

Sporophytes terminal. Setae present, short and broad, 1.2--1.5(2.0) mm long, 0.2--0.4 mm wide, flattened and ridged, in transverse section outermost 3--5 rows of cells round, ± evenly thick-walled, innermost 7--11 rows oval-hexagonal, thin-walled and collenchymatous, central strands absent; foot longly tapering. Capsules elongate-oval when young, at maturity broader and tapering gradually at the apices and abruptly basally, dehiscing by 4--8 irregular longitudinal valves in conic upper part of capsules, valves not reaching apices, margins inrolled when dry, ± plane when wet, capsule shape little changed by changes in moisture; chestnut-brown to shining black in upper valved part, paler below. Exothecial cells quadrate to short-rectangular, sutures of thin-walled cells absent; valve exothecial cells with thick longitudinal and thin transverse walls, triangular in transverse section, the inner bases of the triangular cells very thin-walled, sides very thick-walled. Stomata absent. Annuli, opercula and peristomes absent. Sporogenous tissue and columellae derived from endothecium; spore sacs dome-shaped, overarching massive, rod-like persistent columellae; spores sacs not separated by air spaces from capsule walls. Spore abortion frequent; spores very large, spherical to oval; shriveled brown spores about 52--65 µm, turgid green spores about (50)88--100(122) µm, papillose to reticulate-papillose. Mature in summer. Calyptrae large, 0.9--1.5 mm long, covering entire capsules, often persisting to maturity, yellowish brown, mitrate, but becoming cucullate as they split when capsules widen.

On irrigated limestone, dolomite and calcareous sandstone; cushions often coalescing and forming extensive mats covering many square meters on vertical cliffs. The large black mats area visible for miles on the white limestone cliffs that predominate in the Brooks Range of Alaska. Sporophytes are common in the northern part of its range but are rare in southernmost collections.

Endemic to northwestern North America. Occasional in mountains in arctic Alaska, often locally abundant. Also known from several localities in subarctic Alaska and the Yukon, British Columbia and Northwest Territories.

Selected specimens seen:

Alaska. Kurupa Lake, 68°22'N, 154°39'W; 1974 Iwatsuki 3342 (ALA, NY). - "Mount Hultén", Mile 271 Dalton Highway, 68°27'N, 149°18'W; 1976 Murray 76-254 (ALA). - Mountain W of Galbraith Lake, Mile 275.5 Dalton Highway, 68°27'N, 149°30'W; 1981 Murray 11,114 (ALA). - Upper Sheenjek Valley: Ambresvajun Lake (Last Lake) vicinity, 68°35'N, 143°43'W; 1975 Batten 75-48 (ALA, NY). 8 km N of Ambresvajun Lake; 1975 Batten 75-47 (ALA, NY). 32 km N of Ambresvajun Lake, 68°51'N, 143°28'W; 1975 Batten 75-4 (ALA, NY). - Lookout Ridge, 69°07'N, 158°10'W; 1979 Murray 9222 (ALA). - Lake Peters, 69°22'N, 145°03'W; 1961 Steere 610706-6 (ALA, NY). - Cache

Creek, Ikiakpaurak Valley, 69°25'N, 146°00'W; 1974 Murray 6556 (ALA). - Sadlerochit Mountains, 69°40'N, 145°50'W; 20 Jul 1983 Lipkin s.n. (ALA).

Andreaeobryum macrosporum is easily distinguished from Andreaea species by its occurrence calcareous rock, the broadly conic capsule that tapers abruptly to a stout seta and does not contract in length or bulge when wet, and the very large spores.

Andreaeaceae

A family with one genus.

1. Andreaea Hedw., Sp. Musc. 47. 1801. - Type: A. rupestris Hedw.

Plants small to very large and robust, caespitose, perennial, darkly pigmented, green only when young or shaded. Globose multicellular protonemata formed within stretched spore wall, from which branched thallose protonemata and rhizoids are produced. Leaf-like protonematal appendages observed in several species. Stems from 0.5 to 10 or more cm long, irregularly branched, often by innovations, in transverse section usually of ± uniform thick-walled cells, cortical cells sometimes smaller and thicker walled than inner cells, central strands absent. Rhizoids basal on stems and sometimes branches, filamentous, uni- and biseriate, red-brown. Minute, imbricate scale-like leaves occur frequently along lower portions of stems, on flagelliform shoots or along middle portions of stems. Irregularly shaped primary leaves resembling pseudoparaphyllia can occur at bases of stems and branches. Leaves spirally arranged, larger and denser on upper portions of stems, sometimes eroded along lower portions of stems, usually more spreading when wet, in ecostate species often squarrose, variable in orientation and shape: usually clasping below, ± spreading above, and ± constricted, like a waist, near mid-leaf and apices incurved or secund in ecostate taxa; ± abruptly contracted to the subulae and often secund above in costate taxa; usually somewhat narrowed to a straight insertion, rarely auriculate. Costae, when present, variable in form: single or branched, distinctly or indistinctly delineated, short to excurrent, broad or narrow, strong throughout or lacking apically or basally; in transverse section of ± uniform, thick-walled cells. Laminal cells variable: in ecostate species usually short above, becoming rectangular to elongate below, mid-leaf and basal marginal cells ± differentiated; in costate species often short throughout, some subcostal cells rectangular; laminal cells usually unistratose in ecostate species, usually bi- to multistratose, at least in spots in costate species; transverse walls very thin, longitudinal walls often thick and pitted, rarely thin, smooth or sinuose. Margins usually plane to somewhat incurved, rarely reflexed. Axillary hairs with 1--3(4) quadrate, brown basal cells and 1(2--more in inflorescences) elongate, hyaline or brown cells, the terminal cell cylindrical, often clavate, hyaline or becoming brown with age. Usually cladautoicous, often difficult to demonstrate due to brittle stems; rarely dioicous or gonioautoicous. Paraphyses rare or lacking in gynoecia, few or numerous in androecia. Archegonia terminal, rarely lateral, usually 3--6. Perichaetial leaves large, often differentiated, convolute and sheathing. Androecia terminal or lateral, bulbiform, antheridia usually 4--10, elliptic, on biseriate stalks. Pseudopodia slender, pale brown to black, slightly twisted to the left in surface view.

Sporophytes terminal. Setae absent, sporophytes consist of capsules and bulbous to shortly tapering feet. Capsules when dry contracting in length and valves bulging, when wet elliptic and valves closed; dehiscence by 4 or rarely 8--10 longitudinal valves that reach neither bases nor apices of capsules, margins of valves ± reflexed when dry, plane to inrolled when wet; bases from (1/8)1/4--1/2(over 3/4) the length of the capsules; necks very short, apices usually shortly conic-apiculate. Exothecial cells rectangular to long-rectangular, sutures consisting of thin-walled cells present; valve exothecial cells with thick longitudinal and thin transverse walls, usually oval and with all walls thick in transverse section. Stomata absent. Annuli, opercula and peristomes absent. Sporogenous tissue and columellae derived from endothecium; spore sacs dome-shaped, overarching rod-like persistent columellae; spore sacs not separated by air spaces from capsule walls. Spore abortion rare to frequent; spores small to very large, usually spherical, sometimes angled, (10)13--60(110) µm, usually papillose to reticulate-papillose, rarely almost smooth. Mature from spring to fall. Calyptrae apical, very small, consisting chiefly of unmodified archegonial necks, campanulate-mitrate, usually falling early.

Andreaea probably comprises fewer than 50 species, with the greatest diversity in the Southern Hemisphere. Often called granite mosses, Andreaea species are easily distinguished from Andreaeobryum by their occurrence on acidic substrates and by the capsule that bulges and contracts in length to release spores, the presence of a pseudopodium, and, except for one non-arctic species, by the smaller spores.

Arctic costate species and the denticulate ecostate *A. alpina* present no great difficulties in identification, but the *A. rupestris* group (here treated as *A. rupestris* var. *rupestris*, *A. rupestris* var. *papillosa*, *A. alpestris* and *A. obovata*) is a problem. *Andreaea alpestris* and *A. obovata* have northern distributions and are structurally quite uniform, but *A. rupestris sensu lato*, which is more widespread, is extremely polymorphic and has many properties shared by *A. alpestris* and *A. obovata*. Because of this no one character, such as color, leaf shape and orientation, size, papillosity, cell size, wall thickness or pittedness should be considered diagnostic. In the North, members of the *A. rupestris* group, with the notable exception of *A. rupestris* var. *rupestris*, frequently occur on coarse mineral soil where they are very well developed and robust. In such situations they are easily identified, but small rock populations may cause difficulty.

Invaluable references describing the variation in the *A. rupestris* group are Schimper (in Bruch, Schimper and Gümbel, Bryol. Eur. 6: 131--156, Pl. 1--14(623--636), 1855), Mårtensson (Kungl. Svenska Vetenskapsakad. Avhandl. Naturskyddsarenden 14: 20--28, 1956) and Nyholm (Illus. Moss Fl. Fennoscandia 2: 688--696, Swedish Nat. Research Council, Stockholm, 1969).

The following key includes the most constant group of features by which these taxa can be recognized. In such a variable group, however, it is not unusual for intermediate specimens to occur, and I have taken a broad view of *A. rupestris* and included most such forms within that taxon.

Approximately 1125 specimens of the *A. rupestris* group were examined from 59° N northward from Greenland, Canada and Alaska, of which about one half are from Greenland. About one half of the entire material studied is *A. rupestris* var. *papillosa*, one quarter is *A. rupestris* var. *rupestris*, about 18 per cent is *A. alpestris*, and about 7 per cent is *A. obovata*. *Andreaea alpestris* is quite common in Greenland representing over one quarter of the *A. rupestris* group there, but it is rare in Canada and Alaska where it accounts for about 8 per cent of the group. The ranges of *A. rupestris* var. *rupestris* and var. *papillosa* overlap to a great extent, but the frequency of each differs greatly. Between latitudes 59--63° N the ratio is about 1:1 *papillosa*:*rupestris*, between 64--67° about 2:1, between 68--72° about 4:1 and between 73--76° over 5:1.

Andreaea crassinervia Bruch and *A. rothii* Web. & Mohr have been reported for Greenland, and *A. crassinervia* has been reported from Baffin Island, but all material I have seen is equivocal. It is possible, however, that *A. crassinervia* and *A. rothii* occur in the Arctic, so they are included in the key in brackets.

A specimen in S labeled only *A. crassinervia*, Greenland, Schimper is a mixture of *A. crassinervia* and *A. frigida* Hüb. Both occur in Europe, and other than this incompletely labeled specimen *A. frigida* is not known elsewhere, so I suspect that the specimen is mislabeled. Material in NMW (and duplicates in BM) cited by Wade as *A. crassinervia* (Bryologist 57: 225--229, 1954) from West Greenland is *A. blyttii*. I have not found in BM the specimens collected at Clyde on Baffin Island by Polunin that were determined to be A. crassinervia by W. R. Sherrin and cited as being housed in BM, but not seen, by Steere (in Polunin, Nat. Mus. Canada Bull. 97: 1--573, 1947). It is possible that this material was lost when Sherrin's lab was destroyed during World War II (loc. cit., see footnote 3, p. 375).

Andreaea rothii has been reported from Greenland without substantiation in most general 20th century Floras. I do not know the basis for these citations, perhaps the report by by R. Brown (in Rink [ed. R. Brown] Danish Greenland, p. 420, Henry S. King & Co., London, 1877) who based this catalog of cryptogams of Greenland on mosses collected by Berggren in 1870 and his own list. His report of A. rothii may well refer to Berggren's A. crassinervia var. obtusifolia (= A. heinemannii) as suggested by Lange and Jensen (Meddr. Grønl. 3: 309--446, 1887).

Microscopic diagnostic features are most easily seen when a mounting medium such as Hoyer's, lactophenol or a dilute solution of potassium hydroxide is used.

1. Leaves subulate and costate.
    2. Leaf margins crenate to serrate, with sharp laminal and costal papillae. Perichaetial leaves larger than stem leaves but not differentiated, neither sheathing nor convolute .... 1. A. nivalis
    2. Leaf margins entire or rarely slightly crenate, laminal papillae absent, costal papillae low or absent. Perichaetial leaves differentiated, sheathing and convolute.

3. Spores 11--19(23) µm. Basal laminal cells mostly rectangular, walls little pitted, not sinuose. Dioicous .... 2. *A. blyttii*

3. Spores over 25 µm. Basal laminal cells mostly quadrate, round, rounded-oblate or short-rectangular, walls often pitted and sinuose. Autoicous.

    4. Costae usually weak and flattened above (at most 4-layered), often lacking basally. Usually some basal marginal cells rectangular .... 3. *A. heinemannii*

    4. Costae strong throughout, usually terete above (5--6-layered). Basal marginal cells mostly isodiametric, rarely one or two short-rectangular.

        5. Spores 24--35(40) µm. Transition between laminae and costae indistinct (dorsal costal surface not bulging). Laminae indistinct in subulae, costae often filling subulae .... [*A. crassinervia*]

        5. Spores (30)35--50(70) µm. Transition between laminae and costae distinct (dorsal costal surface bulging). Laminae distinct throughout or at least in lower parts of subulae, costae sometimes filling upper parts of subulae .... [*A. rothii sensu lato*]

1. Leaves ± lanceolate or panduriform, ecostate.

    6. Margins denticulate at leaf bases .... 4. *A. alpina*

    6. Margins entire or weakly crenate at leaf bases.

7. Leaves usually curved to secund, with oblique apices. Papillae usually prominent and whitish, at least dorsally on upper leaves. Upper cell lumina often stellate, rounded or oval, walls usually incrassate, pitted, and collenchymatous. Plants greenish bronze, black or reddish.

    8. Leaves lanceolate or occasionally panduriform, gradually narrowed to short or long, obtuse or acute apices ...... 5. *A. rupestris* var. *rupestris*

    8. Leaves abruptly narrowed from ovate or panduriform bases to long, acute apices .... 5. *A. rupestris* var. *papillosa*

7. Leaves usually straight, apices occasionally oblique. Papillae usually low or absent, very rarely prominent or whitish. Upper cell lumina rounded or stellate, walls incrassate, pitted and collenchymatous or not. Plants characteristically brown, black or reddish black.

    9. Leaves usually asymmetric, ± lanceolate, broadest below mid-leaf, not apiculate. Papillae inconspicuous. Basal cells short-rectangular with broad, bulging lumina, walls little pitted. Upper laminae unistratose or some leaves with central bistratose patches, cell lumina rounded, walls not very collenchymatous or incrassate. Plants black or brown, occasionally reddish black. 6. *A. alpestris*

    9. Leaves symmetric, panduriform, broadest above mid-leaf, ± apiculate. Papillae rarely

conspicuous. Basal cells rectangular to long-rectangular, lumina rarely bulging, walls pitted. Upper laminae unistratose, cell lumina stellate, walls collenchymatous and incrassate. Plants usually reddish or purple-black, occasionally black (when submerged in running water greenish and with distant, often secund leaves) .... 7. _A_. _obovata_

1. _A_. _nivalis_ Hook.

Trans. Linn. Soc. London 10: 395. 1811. - Type: Scotland; holotype and isotypes in BM, seen.

Plants medium-sized to very large and robust, brownish green to red-brown. Stems up to 10 cm long. Leaves when dry erect, curved, secund or falcate-secund, lower stem leaves distant, at stem apices secund or falcate-secund, gradually narrowed from an oblong base to a sharp tip; 1--2 mm long, 0.3--0.5 mm wide. Costae present, single, percurrent or filling leaf apices, strong, about 1/5 the width of leaf bases, tapering gradually or of equal width upwards, distinctly delineated and strong (frequently only costae remaining on lower portions of stems), reddish, dorsally strongly papillose. Laminae unistratose, areolation distinct, many cells papillose dorsally and ventrally. Laminal cells ± uniform, quadrate to rounded, 9--11 µm, occasionally short-rectangular and narrower in leaf bases, thin-walled, not pitted, not collenchymatous. Margins plane to partially reflexed, irregularly denticulate or crenate from papillose cells; auriculate-decurrent.

Dioicous. Upper stem and perichaetial leaves similar to stem leaves but abruptly larger, not sheathing or convolute.

Capsules (not seen in Greenland material) usually with 4 large and 2 small valves that extend to near bases and apices. Spore abortion occasional, spores (18)20--30(40) µm. Chromosome number reported: n=10 (Japan; the report from South Georgia [Fritsch, Regnum Vegetabile 108: 72, 1982] is a transcription error for *A. australis* F. Müll. *ex* Mitt.).

On wet rocks in streams, snow flushes and on seeping outcrops, often forming large mats.

Very rare in the Arctic, known only from southern and southwestern Greenland in our region and reported from Novaya Zemlya. Generally found in alpine regions in oceanic parts of the Northern Hemisphere: recently reported for eastern North America from western Newfoundland (Belland, Canad. J. Bot. 61: 218--223, 1983); in northwestern North America from central Yukon and southern Alaska south to British Columbia, Washington, Oregon, and California. Otherwise known from Europe, the Caucasus, Asiatic U.S.S.R. and Japan.

Specimens seen:

Greenland. Without locality; 1899 comm. J. Macoun (S). - S1: Chr. IV Ø., Tasiussaq, 60°06'N, 43°47'W; 1966 Gravesen & Hansen 66-576 (C). - W3: Sukkertoppen Koloni, 65°35'N, 52°46'W; 1955 Clausen 265 (C, CANM, S).

Easily distinguished by its sharply denticulate and papillose leaf margins and, when fruiting, by the non-sheathing perichaetial leaves. In habit it resembles the hepatic genus Herbertus and the non-costate falcate form of A. rupestris var. papillosa.

2. A. blyttii Schimp.

In Bruch, Schimper & Gümbel, Bryol. Eur. 6: 155, Pl. 13(635). 1855. - Type: Norway; holotype in BM, isotypes in CANM, NY seen.

Plants small to medium-sized, brown to black, bases often brown and apices black. Stems up to 2.5 cm long. Leaves when dry erect, curved or secund, especially at stem apices, brittle, gradually subulate from a narrow oblong or ovate base, 1--2 mm long, up to 0.3 mm wide, the subulae 3--4 times longer than the bases, narrow, often only 2 cells wide apically. Costae present, single, ± terete, ± filling subulae, of up to four layers, weaker and bistratose or occasionally absent basally. Laminae unistratose, or bistratose especially near costae. Upper laminal cells round or quadrate, (9)10--12 µm, not thick-walled or collenchymatous, ± smooth to bulging, papillae rare and low. Basal laminal cells rectangular to short-rectangular, very rarely quadrate, in longitudinal rows, lumina angular, walls slightly incrassate, little pitted. Marginal cells in leaf bases mostly short-rectangular, occasionally a few quadrate or long-rectangular. Dioicous. Perichaetial leaves differentiated, sheathing and convolute.

Spore abortion not seen. Spores small, (11)12--19(23) µm, almost smooth.

Forming mats on wet rocks or alluvium, usually at the edges of snow flushes; substrate often snow covered and in meltwater early in summer and dry later. Sporophytes occasional.

Sporadically distributed in the Low Arctic. Otherwise known from Quebec and Newfoundland in eastern North America and in the West from alpine localities in central and southern Alaska, southern Yukon, British Columbia, Washington, Oregon and California. Known also from arctic Europe and arctic Asia as well as from alpine localities in Scotland, Fennoscandia and Poland. Reported from Iceland.

Selected specimens seen:

Greenland. S1: Ilua Torsukatak, 60°08'N, 44°20'W; 13 Aug 1959 Ellitsgaard s.n. (C). - W5: Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren s.n. (ALTA, B, DUKE, H, NFLD, NY, S, TRH). - W7: Savigssivik (Meteorite Island), 76°00'N, 65°00'W; 1950 Jakobsen 10317 (C). - E3: Angmagssalik district, Begin Ikasaulaq, near Qartulajik, 65°51'N, 37°10'W; 1969 Daniëls & de Molenaar M 69606a (ALTA, C, CANM, H, MO, NFLD). - E5: Scoresbysund district, Havnen, 70°29'N, 21°58'W; 28 Aug 1924, Hagerup s.n. (NFLD, NY).

Canada. Labrador: Crater Lake vicinity, ca. 52 mi WSW of Hebron, 58°02'N, 64°02'W; 1954 Gillett 8909 (CANM). - Northwest Territories: Keewatin district, Southampton Island, Hudson Bay; 9 Aug 1864 Macoun s.n. (S). - Franklin district, Baffin Island, Pangnirtung and vicinity, 66°09'N, 65°44'W; 1980 Belland, Brassard & Bridgland 14595 (NFLD).

Alaska. Seward Peninsula, N slope of Bendeleben Mountains, ca. 65°15'N, 163°30'W; 1948 Sigafoos 1495 (MICH). - Brooks Range, Atigun Pass, Mile 247.5 Dalton Highway, 68°08'N, 149°27'W, 1982 Murray 11,343 (ALA).

Andreaea blyttii differs from other arctic, costate members of the Andreaeales in its very long, narrow subula. In addition, the basal cells are mostly rectangular and the spores are small. Small forms can look superficially like A. crassinervia which has short basal cells and larger spores.

3. A. heinemannii Hampe & C. Müll.

Bot. Zeit. 4: 324, Pl. 2. 1846. - Type: Switzerland; holotype and isotype in BM seen. - A. crassinervia Bruch var. heinemannii (Hampe & C. Müll.) C. Müll., Synops. 1: 10. 1848.

A. angustata Lindb. ex Limpr., Laubm. Deutschl. 1: 144, Fig. 51. 1885. - Type: Austria; isotypes in B, BM, NY, seen. - A. blyttii Schimp. ssp. angustata (Lindb. ex Limpr.) Schultze-Motel, Nova Hedwigia 16: 460. 1969..

A. crassinervia Bruch var. obtusifolia Berggr., Kongl. Svenska Vetenskaps-Akademiens Handl. 13(8): 40. 1875. - Types: Greenland: Godhavn; 1870 Berggren s.n.; isotypes in H, NY, S, TRH, UPS, seen. Kikertak-ø; 1870 Berggren s.n.; not seen. - A. obtusifolia (Berggr.) Kindb., Eur. N. Amer. Bryin. 2: 394. 1897. Hom. illeg., non A.

obtusifolia T. Jens. 1858. - *A*. *obtusifolia* Berggr. *ex* G. Roth, Aussereur. Laubm. 72. 1911. *Hom*. *illeg*. - *A*. *blyttii* Schimp. var. *obtusifolia* (Berggr.) Sharp, in Grout, Moss Fl. N. Amer. 1: 3. 1936.

A. *planinervis* Lindb. *ex* G. Roth, Aussereur. Laubm. 73, Pl. 8, Fig. 2. 1911. - Type: Caucasus; holotype and isotype in S, seen. - *A*. *planinervis* Lindb., in Broth., Enum. Musc. Caucasi. 94. 1892. *Nom*. *nud*.

A. *crassifolia* Luis., Broteria ser. Bot. 14: 22, Fig. 1--7. 1916. - Types: Portugal, not seen; and Spain, isotype in BM, seen.

Plants small to medium-sized, black to brown. Stems 0.5--1.5 cm long. Leaves when dry erect to divergent, occasionally somewhat flexuose or secund, brittle; oblong-subulate, 1.2--1.5 mm long, up to 0.6 mm wide, subulae gradually formed, about 2 times longer than bases, usually 4--6 cells wide and obtuse apically. Costae present, single, ± flattened, ± indistinct, occasionally strong, ± filling the subulae, often lacking basally, of 2--4 layers apically. Laminae unistratose or with bistratose patches, especially near the costae. Upper laminal cells rounded, isodiametric, 11--13 μm, not porose or thick-walled, bulging. Cells at leaf shoulders oblate, basal laminal cells round, oval, oblate to rounded-rectangular. Marginal basal cells rounded or short-rectangular. All basal cells often sinuose. Reportedly autoicous. Perichaetial leaves differentiated, sheathing and convolute.

Spore abortion not seen. Spores angled, 22--32(40) μm.

Occurs most commonly on dry, exposed acidic rock, often with A. rupestris var. rupestris and var. papillosa. Sporophytes frequent.

Rare, in the Arctic previously known only from type material of A. crassinervia var. obtusifolia in West Greenland. In the protologue Berggren cited material from Kikertak-ø, which is a small island in a bay on Nugssuaq Peninsula (70°00'N, 51°19'W). I have seen no material from there, and Berggren (op. cit., p.11--12) does not mention it in his citation of plants from that locality. He does, however, list it for nearby Ritenbenk (p. 11), and I have seen several collections with that locality on the labels. It is possible that the citation from Kikertak was an error, or that the plants were incorrectly labeled from Ritenbenk. I have seen many specimens of Andreaea collected in 1870 by Berggren and none of them are labeled Kikertak even though he cited several species from that locality. Schuster and Damsholt (Medd. Grønl. 199(1): 167, 272, 1974) discussed similar discrepancies in hepatic collections and wrote that the labeling mistake "could easily have been made as Berggren visited the Nugssuaq area only one day and stayed at Ritenbenk both before and after this visit." At any rate, it seems clear that the material labeled Ritenbenk is part of the type material. Material in C and NY collected in Greenland (without locality information) by Raben and cited by Lange and Jensen (Medd. Grønl. 3: 309--446, 1887) as A. crassinervia var. obtusifolia was misidentified and is A. blyttii.

Andreaea heinemannii occurs also in southern Europe, the Caucasus, Canary Islands and Madeira. Previously unknown in North America, I have seen material from Yukon, Alberta, British Columbia, Washington, Oregon, California, and Colorado as well as one Southern Hemisphere collection from Kerguelen Island.

Specimens seen:

Greenland. - W4: vicinity of Egedesminde, Geological Station, 68°42'N, 52°55'W; 22 Aug 1985 Murray _s.n._ (ALA). - W5: Godhavn, mountain NE of Arctic Station, ca. 69°25'N, 53°24'W; 17 Aug 1985 Murray _s.n._ (ALA). - Arveprinsens Island: Laksebugt, ca. 69°43'N, 51°19'W.; 14 Aug 1985 Murray _s.n._ (ALA). Ca. 69°46'N, 51°12'W; 15 Aug 1985 Murray _s.n._ (ALA). - Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren _s.n._ (NY, S, TRH, UPS). - E3: Tasilaq, 66°04'N, 37°02'W; 1970 Lewinsky 70-849 (C). - E5: Liverpool Land: Cape Tobin, 70°25'N, 21°58'W; 12 Jul 1955, Sørensen _s.n._ (C). - Hvalrosbugt, 70°30'N, 21°58'W; 22 Jul 1951 Anderson _s.n._ (C).

Andreaea heinemannii is easily identified by its small size, untidy look due to divergent leaf tips, obtuse leaf tips, the ± flattened subula and the costa often very weak or lacking basally. Its spores are twice the size of those of _A. blyttii_, the subula is shorter and broader, and the basal cells are often rounded, oval or oblate with sinuose walls, not rectangular with mostly evenly thickened walls. _Andreaea crassinervia_ and _A. rothii_, whose presence in the Arctic has not been established, differ in having much stronger costae and isodiametric basal cells, and the spores of _A. rothii_ are larger. _A._

heinemannii has occasionally been mistaken for *A. rupestris* because of its weak costa.

4. *A. alpina* Hedw.

Sp. Musc. 49, Pl. 7, Fig. 2p. 1801. - Types: Europe; not seen.

Plants large, reddish brown to purplish black. Stems up to 4 cm long. Leaves when dry erect, straight, stiff, apices incurved; panduriform, broadest above constriction, about 1 mm long, 0.4 mm wide, symmetrical, abruptly narrowed to triangular apices about 1/4--1/3 the length of leaves. Costae absent. Laminae mostly unistratose, with occasional bistratose patches especially apically, upper cells round to oval, lumina oval, about 5 µm wide, walls thick, about 5--6 µm, somewhat collenchymatous, papillae lacking. Transition from upper to lower cells ± abrupt. Basal cells rectangular to long-rectangular, lumina and walls about the same width, walls pitted and nodose. Margins denticulate from near bases into mid-leaf constriction due to projecting cell ends, appearing bordered by several rows of oblique, thinner walled cells. Perichaetial leaves differentiated, sheathing and convolute.

Spore abortion occasional; shriveled brown spores 17--28 µm, turgid green spores 26--38 µm, rarely larger.

The Greenland specimen has sporophytes; no ecological information was given. Elsewhere usually on wet acidic to basic rocks.

Very rare; new to Greenland, from the southernmost district. Lagerkranz (Nova Acta Regiae Soc. Sci Upsal. ser. 4 14(6): Appendix, Musci, p. 129-134, 1950) reported *A. alpina* for Upernavik and Godhavn in West Greenland. His list is purportedly based on specimens identified by H. Persson. I have seen Lagerkranz collections identified by Persson in S and UPS. None were identified as *A. alpina*; rather the material from Upernavik was correctly identified by Persson as *A. alpestris* and that from Godhavn or Disko as *A. rupestris*. Apparently someone else named some material *A. alpina* or a nomenclatural error was made in assembling the list. For many years *A. alpina* was nomenclaturally confused and many 19th century reports or identifications cannot be relied upon. All early Greenland collections that I have seen identified as *A. alpina* are really *A. alpestris*.

The southernmost Greenland region where *A. alpina* was collected has high summer temperatures and high precipitation, birch and willow copses occur, and a cold-temperate or suboceanic floristic element or vegetation is present. For these reasons, the area is considered subarctic and suboceanic rather than arctic by some biogeographers. *Andreaea alpina* occurs in similar climates elsewhere in the North Atlantic region from the British Isles, the Faroes and Norway. In the Southern Hemisphere it is widely distributed on subantarctic and cold temperate islands as well as along the west coast of South America as far north as Colombia. In the Southern Hemisphere it is part of a group of closely related taxa. In the Northern Hemisphere, however, it is taxonomically uniform and has no close relatives.

Specimen seen:

Greenland. S1: Julianehab district, Kangersuneq qingordleq, Igdlorssuit, 60°21'N, 44°03'W; 1970 Jacobsen 5039 (C).

Easily identified by its large size, rather coarse appearance, and its symmetric, panduriform leaves that are denticulate along the lower margins and have abruptly formed triangular apices.

5. A. rupestris Hedw.

Var. rupestris

Sp. Musc. 47., Pl. 7, Fig. 2g--o. 1801. - Types: Europe; not seen. - A. petrophila Ehrh. ex Fürnr., Flora 10, Beibl. 2: 30. 1827.

A. petrophila Fürnr. var. homomalla Thed., Bot. Not. 5: 79, Fig. 48--54. 1849. - Types: Scandinavia, Germany and Britain; not seen.

Plants medium-sized to large, greenish bronze, reddish brown or black. Stems rarely over 3 cm long. Leaves variable: straight to secund, when dry appressed, spreading, squarrose, or sometimes imbricate, when wet widely spreading to squarrose; ovate- to oblong-lanceolate, little constricted above bases or panduriform, usually broadest below constriction, usually less than 1 mm long and 0.5 mm wide; apices usually oblique, often secund, often incurved, obtuse or acute, short to long, gradually formed. Costae absent. Laminae unistratose, upper cells quadrate to short-rectangular, lumina variable: rounded, oval to irregular, stellate or short-rectangular, about 8--10 µm wide, walls usually thick, 2--6 µm, usually strongly pitted, collenchymatous, characteristically with prominent, whitish cuticular dorsal papillae that are longer than wide. Transition from upper to lower cells ± abrupt. Basal leaf cells variable: short- to long-rectangular, lumina wider or much narrower than walls, bulging or not, walls pitted, sometimes strongly so and nodose. Basal marginal cells quadrate, oblate or short-rectangular. Autoicous. Perichaetial leaves differentiated, sheathing and convolute, usually strongly papillose.

Spore abortion frequent; shriveled brown spores usually 20--24 µm, turgid green spores 26--32(48, rarely more) µm.

Usually forming greenish or black cushions on ± acidic rock that is dry or seasonally wet. Often in drier sites than other *Andreaea* taxa, except the xerophilous *A. heinemannii*, and very rare on soil. Sporophytes frequent.

Occasional to rare, becoming less frequent to the north where it is largely replaced by var. *papillosa*. Widespread in North America, from the Arctic south to North Carolina in the East and to northern California and Colorado in the West, also in the northern tier of midwestern states: Ohio, Minnesota, Michigan, and Wisconsin. Known from Europe, the Caucasus, Asia, Japan and Pacific Islands. Reported from Central and South America, Antarctica, southern Africa, Tasmania and New Zealand.

Selected specimens seen:

Greenland. S1: Narssaq, 60°56'N, 46°03'W; 1962 Steere 62-881 (C, CANM, NY, S). - W5: Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren s.n. (ALTA, H). - E3: Ikasaulaq, 65°59'N, 37°26'W; 1970 Lewinsky 70-1397 (C). - E6: Wollaston Foreland, Daneborg, 74°18'N, 20°12'W; 1947 Holmen 4462 (C).

Canada. Quebec: Hudson Bay, Richmond Gulf, Cairn Island; 1939 Marr M454 (NY). - Northwest Territories: Devon Island, Truelove Lowland, 75°40'N, 84°40'W; 1973 Peterson 2544 (ALTA). Ellesmere Island, Alexandra Fiord, 78°51'N, 75°40'W; Gillett 18335c (NFLD).

Alaska. St. Lawrence Island, Sevuokok, near Gambell, 63°21'N, 169°24'W; 1949 Steere 13690 (ALA, NY). - Etivluk River, vicinity of Etivluk Test Well, 68°22'N, 156°45'W; 1978 Murray 8289 (ALA). - Arctic National Wildlife Refuge, Lake Peters, 69°19'N, 145°03'W; 1974 Murray 6909 (ALA).

The important features that often distinguish this polymorphic taxon are the bronze-green leaves with prominent whitish papillae, the pitted laminal cells, and the gradually formed, usually short and often oblique tip. Var. papillosa usually shares the greenish color and papillae but has a long, abruptly formed leaf tip. Small black forms of var. rupestris with incurved, short, obtuse leaf apices, low papillae and less pitted leaf cells are intermediate to A. alpestris but usually have oblique, unistratose leaf apices some of which are acute.

Andreaea rupestris leaves are often panduriform and almost symmetrical, but they are usually strongly papillose and the tip is usually blunt and oblique, which distinguishes them from *A. obovata*.

Schimper (in Bruch, Schimper and Gümbel, Bryol. Eur. 6: 143, 1855) described eight new varieties of *A. rupestris* (as *A. petrophila*). Several have been reported from arctic regions: vars. *acuminata* (as a synonym of var. *papillosa*), *squarrosula*, *sylvicola* and *pygmaea*. I have not been able to locate unequivocal type material of these varieties, but all material I have seen in Schimper's herbarium at BM is referable to var. *rupestris*. His illustrations of these taxa (Pl. 2(624)) can also be referred to var. *rupestris*. Schimper wrote (op cit. p. 145) that he attached little importance to the distinctions between the varieties he described but that he wished to show the diversity of forms shown by the species as well as to prevent unnecessary naming of new species.

Var. *papillosa* (Lindb.) Podp.

Conspectus Musc. Eur. 45. 1954. - *A. papillosa* Lindb., Ofversigt K. Vet.-Akad. Forhandl. 23: 557. 1867. -Types: Spitzbergen; syntypes in H, BM, TRH, UPS, seen. - *A. rupestris* Hedw. ssp. *papillosa* (Lindb.) C. Jens., Skand. Bladmossfl. 4. 1939. - *A. obovata* Thed. var. *papillosa* (Lindb.) Nyh., Illus. Moss Fl. Fennoscand. 2: 691. 1969.

A. papillosa Lindb. var. *gracilis* Lindb., Ofversigt K. Vet.-Akad. Forhandl. 23: 558. 1867. -Type: Spitzbergen; holotype in H, seen.

A. sparsifolia Zett., Monogr. Andreaearum Scand. 32. 1855. - Type: Norway; in UPS, BM, S, seen. - *A. obovata* Thed. var. *sparsifolia* (Zett.) Nyh., Illus. Moss Fl. Fennoscand. 2: 691. 1969.

A. obovata Thed. var. *acuminata* Lindb., Ofversigt K. Vet.-Akad. Forhandl. 23: 557. 1867. - Type: Spitzbergen; in H, BM, S, seen.

A. patens C. Müll., Bot. Centralbl. 16: 61. 1883. - Type: U.S.S.R., Chukchi Peninsula; isotypes in BREM, H, S, seen.

A. compacta C. Müll., Bot. Centralbl. 16: 62. 1883. - Type: Chukchi Peninsula; isotypes in BREM, H, S, seen.

A. cuspidata C. Müll., Bot. Centralbl. 16: 62. 1883. - Type: Chukchi Peninsula; isotypes in BREM, H, S, seen.

A. assimilis C. Müll., Bot. Centralbl. 16: 63. 1883. - Type: Chukchi Peninsula; isotypes in BREM, H, S, seen.

Plants small, or (on soil) commonly large and robust. Stems often over 3 cm long. Leaves up to about 2 mm long and 0.6 mm wide, apices acute, often very long and abruptly formed from ovate bases; with prominent whitish cuticular papillae often over twice as long as wide or with low, inconspicuous papillae.

Forming dark greenish or black cushions or mats on acidic rock or on coarse mineral soil in snow flushes and streams. When in streams often strongly falcate, with few sporophytes and often mixed with the green secund form of *A. obovata*.

Common in the Arctic and the only *Andreaea* taxon occurring in the North American High Arctic. Primarily an arctic or mountainous taxon at high latitudes; only a little material has been seen from south of our region, from mountains of southern Canada and northern U.S.A. Known also from mostly northern and arctic localities in Europe and Asiatic U.S.S.R.

Selected specimens seen:

Greenland. W5: Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren s.n. (CANM, H, NY, S, TRH, UPS). - W6: "Kekertok", 73°44'N, 56°30'W; 14 Sep 1886, Ryder s.n. (ALA, ALTA, C, NY). - E5: Charcots Land, 71°54'N, 29°00'W; 1958 Holmen 18384 (ALA, ALTA, C, NFLD, NY).

Canada. Northwest Territories: Keewatin district, Chantry Inlet, Parsons Lake, 67°27'N, 95°10'W; 1959 Thomson and Larsen 5948 (NY). - Devon Island, Truelove Lowland, 75°40'N, 84°40'W; 1972 Vitt 5464 (ALA, ALTA, CANM, MO, NFLD, NY, S). - Ellef Ringnes Island, 1.5 mi SSW of Isachsen, 78°46'N, 103°35'W; 1960 Savile 4123 (NY). - Ellesmere Island, The Dean Mt., 82°30'N, 62°20'W; 1973 Brassard 8152 (NY, NFLD).

Alaska. Ogotoruk Creek vicinity, Steep Mt. 68°05'N, 165°37'W; 1980 Murray 10,264 (ALA). - Brooks Range, Chandler Lake, 68°12'N, 152°47'W; 1966 Smith A926 (ALA, BM, CANM, NFLD, NY). - Arctic National Wildlife Refuge, Lake Peters, 69°19'N, 145°02'W; 1974 Murray 6868 (ALA).

Distinguished from var. rupestris by the much longer and more abruptly formed leaf apices and by its frequent occurrence on soil as well as rock. Small rock forms with some leaves with gradually formed long apices are difficult to treat, and taxonomic decisions are arbitrary.

Var. papillosa is just as variable in form as var. rupestris. Falcate forms that have been traditionally treated as A. sparsifolia, and which superficially resemble A. nivalis, occur most frequently in streams, but they also occur with straight-leaved forms on rocks. As in var. rupestris (and many other species of Andreaea) falcate or secund forms are common, and taxonomic recognition does not seem justified. Most of the robust material growing on wet soil presents little difficulty in identification, but occasionally populations with green-bronze, highly papillose but shorter tipped and strongly panduriform leaves are seen in Greenland (these forms are not uncommon in Scandinavia), and the leaf shape resembles A. obovata. Nyholm (Illus. Moss Fl. Fennoscand. 2: 691, 1969) has illustrated such a plant. Panduriform leaves are not uncommon in var. rupestris and well-developed whitish papillae are not characteristic of A. obovata, so I have treated var. papillosa as closer to var. rupestris than to A. obovata, but not without hesitation. I suspect that A. rupestris, A. obovata and A. alpestris may produce similar long-tipped forms; distinguishing them, however, will not be possible without experimental work. In Alaska the most common form of var. papillosa occurs on rock. It consists of material with a very long, abruptly formed subula from an ovate base. The basal cells have extremely thick longititudinal walls and relatively narrow lumina.

Other than the longer and more abruptly formed apices, there is little to distinguish var. papillosa from forms of var. rupestris morphologically, and it is possible that the variation is clinal. Var. *papillosa* has a more northern distribution and much greater frequency northward, and on that basis, as well as its distinctive robust appearance throughout much of its range, it seems deserving of taxonomic recognition.

6. *A. alpestris* (Thed.) Schimp.

In Bruch, Schimper & Gümbel, Bryol. Eur. 6: 146. 1855. - *A. petrophila* Fürnr. var. *alpestris* Thed., Bot. Not. 5: 79, Fig. 45--47. 1849. - Type: Scandinavia; in S, UPS, ALTA, seen.- *A. rupestris* Hedw. var. *alpestris* (Thed.) Sharp., in Grout, Moss Fl. N. Amer. 1: 2. 1936. - *A. rupestris* Hedw. ssp. *alpestris* (Thed.) C.Jens., Skand. Bladmossfl. 4. 1939.

A. filiformis C. Müll., Bot. Centralbl. 16: 62. 1883. -Type: U.S.S.R., Chukchi Peninsula; isotypes in BREM, seen.

Plants medium-sized to large, characteristically brown, brown-black to black, occasionally reddish. Stems up to 4 cm long. Leaves when dry imbricate and appressed, very rarely secund distally; lanceolate, usually little constricted above bases, rarely panduriform, 0.5--1.0 mm long, rarely longer, 0.25--0.4 mm wide, apices straight or occasionally oblique, short, incurved, obtuse, rarely acute. Costae absent. Upper laminae unistratose or often with irregular, central bistratose patches, cells regular, ± quadrate, lumina rounded to oval, (7)8--10(11) um wide, walls usually thin, 2--3(rarely to 6) um, not pitted, weakly collenchymatous, papillae present but low, usually inconspicuous. Cells very gradually becoming longer toward leaf bases. Basal cells short-rectangular, lumina often bulging, up to twice as wide as walls, walls weakly pitted. Basal marginal cells oblate, rounded or short-rectangular. Reportedly autoicous. Perichaetial leaves differentiated, sheathing, convolute, without or with low, very rarely whitish papillae.

Spore abortion frequent; shriveled brown spores 16--21 um, turgid green spores (21)22--26(32) um, very rarely over 30 um.

In wet to dry, or seasonally wet habitats; forming large cushions on wet rock or on silt over rocks in ± level snow flushes; occasionally mingled with _A_. _obovata_. In Alaska at least, it is the only _Andreaea_ species that fills tundra pools and frost scars, and it is rare where water flows faster, on flushed slopes and in streams, where _A_. _rupestris_ var. _papillosa_ and large forms of _A_. _obovata_ occur. Sporophytes uncommon.

Quite common in Greenland, but rare in arctic Canada and Alaska. Reported in Holocene lake sediments dating from about 8000--3000 bp and at present in southernmost Greenland (Fredskild, Jacobsen and Røen, Meddr. Grønl. 198(5): 1-44, 1975). A northern species, occurring elsewhere in North America in mostly oceanic regions: in the East from Labrador and Newfoundland and in the West from subarctic Northwest Territories, the Yukon, Alaska, British Columbia and California. Known from northern Europe and arctic U.S.S.R. Reports from Madeira and southern North America need verification. Material named _A_. _alpestris_ seen from Central and South America is misidentified.

Selected specimens seen:

Greenland. S1: Head of Amitsuarssuk Fjord, 60°46'N, 45°14'W; 1974 Holmen 74-436 (ALA, C). - W4: Christianshaab, 68°49'N, 51°10'W; 1956 Holmen 15,457 (C, CANM, H, S, UPS). - W5: Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren s.n. (C, NY, S, UPS). - W7: Qanaq, Piulip Nuna, 77°28'N, 69°30'W; 1979 Frahm 792393 (C). - E3: Tugtilik, 66°20'N, 35°00'W; 1971 Lewinsky 71-917 (C). - E5: Charcots Land, 71°54'N, 29°00'W; 1958 Holmen 18,402 (C).

Canada. Quebec: Ungava Bay, offshore island, 59°08'N, 65°45'W; 1975 Weber 1408 (H). - Northwest Territories: Ellesmere I., Glacier Valley, 1899 Simmons 944 (H).

Alaska. St. Lawrence I., 63°30'N, 170°30'W; 31 Jul 1879, Kjellman s.n. (S). - Ogotoruk Creek, 68°05'N, 165°40'W; 1959 Johnson, Viereck and Melchior 464 (ALA, S).

A. alpestris is morphologically uniform. Important features are the imbricate leaves that are usually a soft brown-black shade, occasionally a glossy black. The leaf apices are usually obtuse, straight and incurved; and papillae, though present, are low -- not white or conspicuous. Microscopically, it is characterized by thin-walled, little pitted cells with rounded lumina, and in many specimens some leaves have bistratose patches in the upper lamina.

Size of plants is not a good character. Andreaea alpestris is frequently described as much smaller than other Andreaea species, but this is only relatively true. Its leaves are always much smaller and darker in color than A. obovata when they occur together, but on soil it forms long stems and its leaves may be as large as those of A. rupestris and A. obovata on rock. Similarly, leaf cell size is variable. Small forms of A. alpestris on rock can be very difficult to distinguish from forms of A. rupestris, and sometimes a satisfactory determination is impossible. Large soil forms with panduriform leaves and more porose cells are very near A. obovata but can often be distinguished by bistratose areas of the upper lamina and the less symmetrical shape and less strongly pitted and nodose cells.

7. A. obovata Thed.

Bot. Not. 5: 78, Fig. 27--36. 1849. - Type: Sweden; in S, H, UPS, BM, seen. - A. rupestris Hedw. ssp. obovata (Thed.) C. Jens., Skand. Bladmossfl. 4. 1939.

A. hartmannii Thed., Bot. Not. 5: 77, Fig. 1--17, 3--26. 1849. - Types: Sweden; in S, H, UPS, BM, seen. - A. obovata Thed. var. hartmanii (Thed.) Nyh., Illus. Moss. Fl. Fennoscand. 2: 691. 1969.

A. thedenii Schimp., in Bruch, Schimper & Gümbel, Bryol. Eur. 6: 150, Pl. 8(630). 1855. - Type: Norway; in BM, H, seen. - A. obovata Thed. var. thedenii (Schimp.) C. Jens., Skand. Bladmossfl. 4. 1939.

A. obtusifolia T. Jens., Vid. Medd. Naturh. For. Kjobenhavn 1858: 55. 1859. - Type: Norway; isotypes in H, NY, seen.

A. krauseana C. Müll., Bot. Centralbl. 16: 63. 1883. - Type: Chukchi Peninsula; isotypes in BREM, S, seen.

Plants medium-sized to very large and robust, characteristically red-brown, purple-red to purple-brown, often with an orange tint;

greenish when submerged. Stems up to 10 cm long. Leaves straight and crowded or, when submerged in streams, secund and distant; when dry ± appressed; panduriform, broadest above constriction, or obovate, up to about 1.2 mm long, 0.5--0.7 wide, apices usually symmetric, ± abruptly formed and narrow, about 1/4 the length of leaves, or broad and short; margins plane or ± incurved. Costae absent. Laminae unistratose, upper cells ± quadrate, lumina stellate to rhomboidal, 8--10(11) μm wide, walls thick, 5--8 μm, strongly pitted and collenchymatous, papillae very low, usually broader than high, usually inconspicuous or absent. Mid-leaf cells at constriction ± distinct. Basal leaf cells rectangular to long-rectangular, lumina not bulging, usually as wide as or wider than walls, walls strongly pitted and nodose. Basal marginal cells rectangular. Autoicous. Perichaetial leaves differentiated, sheathing and convolute, usually without or with low papillae, rarely conspicuously papillose.

Spore abortion frequent; shriveled brown spores (17)20--23(26) μm, turgid green spores (22)26--35(40) μm.

Forming soft, orange-red, wine-colored or purple-black cushions on seasonally irrigated rocks or soil. Locally abundant in mountain streams are submerged forms with green-black, ± distant leaves that are often secund at stem apices. Such forms are often associated with the falcate form of _A_. _rupestris_ var. _papillosa_. Sporophytes occasional or frequent in populations of robust purple-black plants growing on permanently seeping slopes.

Very rare in North America and rare to occasional in Greenland. Found in low arctic and alpine regions, as far north as 76° N in Greenland and not seen much south of 60° N in Labrador and British Columbia. Known also from northern Europe and Asia. Reported from equatorial Africa.

Selected specimens seen:

Greenland. S1: Igdlokasik Island, 60°47 N, 46°25 W; 1962 Holmen 62-234 (C). - W3: Itivdleq, 64°21 N, 50°27 W; 1973 Lewinsky 73-452 (C). - W4: Egedesminde distr., Inugsulik, 68°18'N, 53°30'W; 4 Aug 1887 Hartz s.n. (NY). - W5: Ritenbenk, 69°46'N, 51°20'W; 1870 Berggren s.n. (C, H, NY, S, TRH, UPS). - W7: Thule; 1953 Benninghoff & Robbins 7696 (NY). - E3: Torssukatak (Tunok), 65°53'N, 36°53'W; 1969 Holmen 69-393 (C, CANM, H, NY). - E5: Liverpool Land, E side of Hartz Vig, 70°27'N, 21°48'W; 1971 Corner, Halliday & Waterston B55f/71 (NFLD).

Canada. Labrador: Nachvak Fjord, Tasuiyak Arm, 59°02'N, 64°03'W; 1975 Weber 1582 (ALTA, H, S). - Northwest Territories: Baffin Island, Clyde R.; 1950 Baird 500624 (NY).

Alaska. St. Lawrence Island, SE of Paavokjaak [Povohok, ?Powooiliak Camp], 63°22'N, 171°17'W; 1933 Geist s.n. (S). - Arctic National Wildlife Refuge: Lake Peters, 69°19'N, 145°03'W; 1974 Murray 6867 (ALA).

A variable species. Small forms of A. obovata on rock are distinguished from other members of the A. rupestris group by their symmetrical, shortly apiculate, panduriform leaves that are clearly wider above the middle and usually lack obvious papillae. They have a characteristic soft wavy look, due to a strong contraction at the waist or mid-leaf region, and tend to be more orange and purple than the other taxa. Occasionally mingled with A. alpestris, leaves of A. obovata are always much larger and usually redder; in addition it can be distinguished microscopically by extremely pitted and collenchymatous cell walls. Symmetric, panduriform, papillose material that is intermediate between A. obovata and A. rupestris var. papillosa occurs occasionally in Greenland.

In permanently wet sites, material is larger and the leaf apicula are shorter and broader or sometimes lacking. In swiftly running water a very distinctive form, traditionally treated as A. hartmannii, occurs; it has a greenish color, long stems, distant leaves and short, secund leaf apices.

VI. THE GENUS ANDREAEA IN BRITAIN AND IRELAND

Introduction

Andreaea is a genus of fewer than 50 species, which are distributed primarily in cool-temperate, oceanic and subpolar regions of both Hemispheres. Species extend to polar areas and also occur in the tropics and subtropics, but only on the highest mountains. In Europe and North America (north of Mexico) I recognize 14 species (see keys in Murray 1986, Chapter IV), of which 11 are present and one more is of doubtful occurrence in the British Isles. Because greatest species diversity occurs in mountainous, oceanic temperate regions, the *Andreaea* flora of the British Isles is about as rich as any in the Northern Hemisphere.

Dillenius (1741), in the first paper entirely devoted to the classification of bryophytes, described (in the genus *Lichenastrum*), from Wales, two present-day species of *Andreaea*, *A. alpina* Hedw. and *A. rothii* Web. & Mohr (ssp. *falcata* [Schimp.] Lindb.). In 1811 British species of *Andreaea* were increased to four when W. J. Hooker described *A. nivalis* from Scotland and listed *A. rupestris* Hedw. Hooker (1811) also described two new varieties of *A. alpina* and one of *A. nivalis*. In the mid-1800s, from about 1830 to 1885, several new costate species were described from Europe, including *A. frigida* Hüb., *A. crassinervia* Bruch, *A. falcata* Schimp., and *A. huntii* Limpr. Schimper (in Bruch, Schimper & Gümbel 1855) also named many new varieties of *A. rupestris* (under *A. petrophila* Ehrh.). Over the years, all of these species and many of the varieties were included in British moss floras--the species often as various synonyms at various ranks (e.g. Lindberg 1870, Braithwaite 1880-1887). In The British Moss-Flora, Braithwaite (1880-1887) also added a new British variety of A. rothii (var. hamata Lindb. ex Braithw.).

In earlier British treatments of Andreaea still considered useful, Braithwaite (1880-1887) accepted five species and 19 varieties, which Dixon & Jameson (1924) changed to four species, one subspecies, and 14 varieties. In the current Moss Flora of Britain and Ireland, Smith (1978) followed Schultze-Motel's (1970) monograph for costate taxa and Nyholm's (1969) treatment for Fennoscandia for ecostate taxa. He recognized six species, four subspecies and five varieties. In the present revision I treat 11 species, three subspecies, and two varieties. Among the species are two that have recently been described, A. sinuosa B. Murr. (Murray 1987) and A. megistospora B. Murr. (Chapter IV), one previously reported only from the Southern Hemisphere, A. mutabilis Hook. f. & Wils., and one, A. blyttii, whose occurrence in the British Isles has been in doubt.

The remaining differences from prior treatments largely result from taxonomic realignments caused by my selection of different characters to those used in the past. As Smith (1978, p. 79) stated: "Some of the species of Andreaea...do not seem to have been properly understood in Britain and the distributions of A. crassinervia and of the varieties of the other species require revision as many gatherings have been incorrectly named." This is indeed so. I have found the main reason for misidentifications is that taxa have been misunderstood. Confusion has centered in large part around A. crassinervia and A. rothii.

The main taxonomic problems in the genus *Andreaea* result from the fact that traditionally used leaf characters have variable states that tend to recur in different lineages, thus they are not particularly reliable and should not be used as primary diagnostic features. Instead, in many cases I have found spore size to be the most useful criterion on which to base taxonomic judgments (Chapter IV).

The aims of this study are to revise the taxonomy of the species of *Andreaea* of Britain and Ireland and to try to make it possible to identify them without much trouble. *Andreaea hartmannii* Thed. (= *A. obovata* Thed.), a species of doubtful occurrence in the British Isles (see discussion under *A. blyttii*), is not treated here, but it is included in the key in square brackets, since there is no reason it should not be found in the region. For members of sect. *Nerviae* Card. *ex* Broth., the key to taxa stresses spore size, since it is the most reliable and useful character. To make easier comparison of all diagnostic features, a comparative table for members of sect. *Nerviae* is also included. For all taxa illustrations of diagnostic features and discussions of field and microscopic characters are provided.

Materials and Methods

This study is based on approximately 2400 herbarium specimens. In addition to my own collections, I have studied material in several principal herbaria in Britain and Ireland: BBSUK, BM, DBN, E, and NMW. Material seen incidently from other herbaria is also cited. Specimens were annotated, and data from labels were recorded for mapping. David

G. Long, Royal Botanic Garden, Edinburgh, organized the label data and (with the help of A. R. Perry, National Museum of Wales, Cardiff, for Wales and parts of England and D. M. Synnott, The National Botanic Gardens, Dublin, for Ireland) prepared vice-county and national grid references for about 1700 collections representing all known localities for each taxon. These records were submitted to C. D. Preston, Institute of Terrestrial Ecology, Natural Environment Research Council of Great Britain, Huntingdon for deposit in the Institute's Biological Records Centre and the production of machine-plotted distribution maps. In this paper, under each species, records are abstracted, with at least the number and location of specimens noted. Numbers in parentheses show numbers of specimens examined. Herbarium abbreviations follow Holmgren *et al*. (1981). Records are cited more completely if the species was recently described, is known from ten or fewer collections in Britain and Ireland, or is new for a vice-county. British and Irish vice-county names and numbers follow those of Corley & Hill (1981), whose catalogue can be consulted for their locations.

Herbarium specimens were supplemented by brief field study in 1982, 1984 and 1985, mostly in Scotland and totalling about two weeks. All but two of the species treated (*A*. *crassinervia* and *A*. *frigida*) have been seen and studied there in the field.

I have seen most types, but for most names, I am still studying typification problems. Synonymy includes names used in Britain and Ireland or elsewhere commonly used.

The descriptions and illustrations of the taxa are based mainly on specimens from the British Isles, supplemented by extra-territorial material, especially if local material is scant. Range of spore size was measured from material mounted in Hoyer's solution and is expressed in terms of normal range of variation, with extremes in parentheses. In general, diagnostic features requiring microscopic study are more easily seen when cleared in a mounting medium such as Hoyer's.

Major Diagnostic Structural Features

General features that apply to the genus _Andreaea_ as a whole have been discussed previously (Chapter II); comments here apply to those that distinguish British and Irish taxa. Most structures are illustrated in the figures.

Axillary hairs. Costate species with differentiated, convolute perichaetial bracts (subg. _Andreaea_ sect. _Nerviae_) and a few ecostate species, e.g. _A. sinuosa_, have axillary hairs that tend to persist, with the upper mucilaginous cells becoming brown. In other species, young hairs, with hyaline mucilaginous cells, are apparent only in actively growing regions (stem apices and gynoecia); with age the terminal mucilaginous cells often disappear and only the quadrate, brown stalk cells are visible along stems.

Leaves. _Andreaeae_ have several kinds of leaves: 1) ordinary mature leaves, 2) reduced, scale-like juvenile leaves, and 3) primary leaves (Fig. VI-12d), which are irregular leaves or filaments, resembling pseudoparaphyllia of pleurocarpous mosses and protonemal appendages of _Andreaea_ (Fig. VI-2i), that are usually seen at the extreme bases of stems and branches. Juvenile and primary leaves are discussed further in Chapter II and are not necessary to distinguish taxa.

Traditionally, characters of mature leaves have been used to differentiate taxa, since capsules rarely prove useful. Leaf attitude, shape, length of tip, degree of papillosity and denticulation, and cell size and wall architecture are characters emphasized. Unfortunately, most species are polymorphic. Leaves vary within a population and even on the same plant; so although leaf features are helpful in delineation of taxa, overemphasis on one or two characters can lead to misunderstanding. For example, in the *A. rupestris* group (including *A. alpestris* [Thed.] Schimp. and *A. obovata*), whether leaves are more or less lanceolate or panduriform and whether the leaf tips are long or short have been considered primary diagnostic features. *Andreaea alpestris* and *A. obovata* are structurally relatively uniform and unvarying. But, *A. rupestris* is polymorphic; leaves are extremely variable in attitude and shape, ranging from erect to strongly falcate and lanceolate to panduriform, with short to long tips that are gradually or abruptly formed. The same degree of variability also applies to characteristics of cell walls. In *A. alpestris* cell walls are usually moderately incrassate, weakly pitted, not strongly collenchymatous, and papillae are absent or inconspicuous. In *A. rupestris* cell walls are usually strongly incrassate, collenchymatous and pitted, and papillae are often present and range from low to high in relief. However, in both species, specimens or even leaves on one plant may have variable pit characteristics, and almost all species of *Andreaea* are variable with respect to stance and length of leaf tip and papillosity, so these characters are often not useful in defining species.

In costate species further characters have been used, the major one being the ratio of lamina to costa in the upper part of the leaf. Some species in sect. *Nerviae* have been defined almost exclusively on this basis, but since the expression of this character is variable within most species, reliance on it leads to difficulty. See discussion under *A. rothii* ssp. *falcata*.

Sinuose basal cell walls are frequent but not obligate in sect. *Nerviae*. *Andreaea sinuosa* (Murray 1986) is the only ecostate species in which this feature is known, and its cell walls are always strongly sinuose. Sinuose walls are known elsewhere in mosses only in the Grimmiaceae, and Noguchi (1974) suggested that in *Racomitrium*, sinuosity is an adaptation to dryness. Another putative adaptation to dryness is the occurrence of what has been termed joint thickenings, that "are developed strictly on both ends of the vertical walls...in the cross-section of the leaf, namely at the spots (joints) where vertical walls come across the free walls of laminal cells...." (Deguchi 1979, p. 136 and Fig. 5a). Known in Grimmiaceae, Dicranaceae and Seligeriaceae, they also are here reported for *Andreaea*, occurring in *A. sinuosa* and *A. blyttii* and also seen occasionally in specimens of other members of sect. *Nerviae*. When I described and figured them previously (Murray 1986), I had overlooked Deguchi's term and description and referred to them inaccurately as micropapillae.

Andreaea nivalis demonstrates several features of subg. *Chasmocalyx* (Braithw.) Lindb. that are not found in other *Andreaeae* of the British Isles: small, thin-walled leaf cells, auriculate leaf bases, and on occasion partially recurved or incurved leaf margins. Most

Andreaeae have incrassate cell walls, straight leaf insertions, and incurved leaf margins.

Sexual condition. Andreaea nivalis, A. blyttii, and possibly A. sinuosa are dioicous. Other species in the British Isles are cladautoicous, the more common condition. Members of sect. Nerviae are often gonioautoicous as well as cladautoicous.

Perichaetial bracts. Subgenus Chasmocalyx, represented by A. nivalis, has large perichaetial bracts that are not otherwise significantly different from mature vegetative leaves. When capsule development begins, the upper part of the stem lengthens, and leaves along the upper stem are larger and more distant than on sterile stems. In other species of Andreaea, development differs from that of subg. Chasmocalyx. The leafy stem elongates much less when capsule development begins, and several closely inserted, convolute bracts mature and enclose the young capsule.

Pseudopodium. In Andreaea the capsule is elevated at maturity on a stalk of gametophytic origin, the pseudopodium. In subg. Chasmocalyx, the pseudopodium is evidently formed not only from archegonial tissue and the stalk (or pedestal) that subtends the archegonium, but also partly from stem tissue, since unfertilized archegonia, small bracteoles, and axillary hairs are often observed high on the pseudopodium. In other Andreaea species, the mature capsule is elevated on a pseudopodium in which stem tissue is a minor component. Only occasionally are unfertilized archegonia seen on the lower part of the pseudopodium, never well up the stalk, and I have not observed leaves of any sort or axillary hairs on the surface of the pseudopodium.

Capsule. In *Andreaea* the capsule dehisces by means of longitudinal valves that remain coherent at the capsule apex (unless tissue disintegrates with age) and that extend a variable distance toward the base of the capsule. Typically, four more or less regular valves are formed. The ratio of base to valve length varies. In most British and Irish species the base occupies at least one third the length of the capsule and in *A. sinuosa* over one half. In *A. nivalis* the valves number up to six and often extend to near the base of the capsule. As a result, when dry the valves bulge and the capsule becomes almost globose, truly resembling a Chinese or Japanese lantern. (Lantern mosses is one of the common names used for the genus.)

Spores. In most *Andreaeae*, spores remain in tetrads until the capsule is almost mature, and a large, but irregular percentage of the spore mass aborts, resulting in two classes of spores: one composed of brown, shrivelled, relatively small spores; the other of green, turgid, relatively large spores. Members of sect. *Nerviae* are an exception; in this group spores separate early, and spore abortion occurs rarely and involves a very small proportion of the spore mass. It seems likely that this is the derived condition in *Andreaea*.

For the most part, spore size has been considered unimportant in the classification of *Andreaeae*. To the contrary, I have found it a most useful criterion for defining many taxa--the most useful for many that occur in the British Isles, since the expression of most leaf characters varies. Since spores of all Andreaea species germinate within the spore wall, often prior to dehiscence of the capsule, a small or large cell mass can result and the size range of living spores within a capsule can be large (Chapters II and IV).

Since spore size is such an important character, it should be noted that even when mature capsules are not evident, spores can often be seen among old perichaetial bracts or in the bases of eroded capsules. Also, because spores in Andreaea reach mature size early in capsule development, hyaline or tan spores in green capsules can sometimes be used to determine general spore size.

Chromosome Numbers

Cytological information about Andreaea is scant. The number n=10 has been counted for six species, including extra-territorial material of species found in the British Isles: A. nivalis, A. rothii (recently identified by me as ssp. rothii), and A. rupestris (Fritsch 1982). The only counts made on British material are by Smith & Newton (1968). Their discovery that Welsh material of A. rothii (recently identified by me as ssp. falcata) had a count of n=11, shows that cytological work may prove helpful in delineation of taxa.

Ecology

The ecology of Andreaea has been little studied; the phrase, heavy metal and acid rock, about sums it up and has a nice ring to it. The genus Andreaea is usually given the common name, granite mosses. Andreaeae do tend to occur on acidic rock, but some species grow often on mildly basic rocks, e.g. A. alpina. Differing ranges of pH, between about 4 and 7, have been reported for substrates of a few Andreaea species from outside Britain and Ireland, which shows that the taxa may sort out along gradients of pH (Amann 1928, Elvebakk 1984). In Scotland, on the Isle of Skye, A. rothii has been reported as indifferent to rock type, only avoiding lime (Birks & Birks 1974), but there appear to be other interesting aspects to its substrate ecology. In North Carolina, Rohrer (1982) found that A. rothii was one of few bryophytes restricted to a single rock type. And Bates (1978) reported that Hebridean material of A. rothii has an unusual ability to accumulate heavy metal; plants were found to have high iron and aluminum contents when growing on Torridonian sandstone, which is low in these elements.

Species diversity in Andreaea is greatest in mountainous regions with oceanic or humid, cool-temperate climates. I have recorded 14 taxa from British Columbia, 13 from the British Isles, and 12 from Norway and the Alps, as compared with eight for the Arctic, seven for southern Europe, and six for the eastern and conterminous western United States. From these data it is apparent that features of regional climate, especially moisture and temperature, are important in determining geographic patterns. However, Andreaea species are also among the most tolerant mosses in terms of environmental extremes. Dilks & Proctor (1975) found that certain Andreaea species were extremely resistant to freezing and yet A. rothii and A. alpina also showed substantial net assimilation at temperatures as high as 40°C.

Many *Andreaea* species occur in habitats that are exposed to wide extremes of moisture and shade, being wet or submerged early in the growing season and dry and exposed later. Their physiological tolerance enables them to succeed in very severe as well as variable conditions. This tolerance could permit survival during major climatic change such as has occurred in glacial and interglacial intervals.

As with *Sphagnum* and *Drepanocladus*, for example, it is common for closely related species or infraspecific taxa of the same species of *Andreaea* to grow in close association. For example, in Scotland, at the Pass of Glencoe, I have seen six taxa growing within a few feet of each other, some mingled. With its diverse *Andreaea* flora and juxtaposed species in easily accessible locations, the British Isles is an ideal place to study the autecology of *Andreaeae*.

Andreaea species of the British Isles comprise three groups in terms of range of elevation: 1) those occurring only in mountains, close to summits, often in snow-beds or -flushes and rarely seen much below 900 m: *A. nivalis*, *A. blyttii*, *A. crassinervia*, *A. frigida*, *A. sinuosa*, and *A. alpestris*; 2) those occurring from near sea level and reaching the alpine but rarely seen much above 900 m: *A. rothii* and *A. megistospora*; and 3) species more or less indifferent, found from near sea level to mountain summits: *A. alpina* and *A. rupestris*. *Andreaea mutabilis* can be placed in this last group, but most collections are from the alpine, and it is rarely seen below 600 m (several collections are from 150-250 m).

Distribution

The geographic distributions of the 13 taxa of *Andreaea* in the British Isles form interesting patterns because they show endemism and wide disjunctions of several types:

1. *Widespread in the Northern Hemisphere*: *A. rupestris* var. *rupestris*. *Andreaea rothii* ssp. *rothii* occurs in Europe, eastern and western North America and has been reported from Mongolia, so may generally fit this pattern, although there are large gaps in its distribution.

2. *Circumalpine* (*sensu Schofield 1980*) *or circumpolar taxa*: *A. nivalis*, *A. blyttii*, *A. rupestris* var. *papillosa*, and *A. alpestris*.

3. *Amphi-Atlantic species*: *A. crassinervia*.

4. *Northwestern European-Northwestern North American disjuncts*: *A. megistospora* ssp. *megistospora* and *A. sinuosa*. The pattern of *A. rothii* ssp. *falcata* may be similar; it is widespread in Europe, but I have seen only one North American collection, from Oregon.

5. *Bipolar species*: *A. alpina*. *Andreaea mutabilis* also occurs in both hemispheres, but not as widely disjunct as *A. alpina*. In tropical and subtropical regions *A. mutabilis* occurs only on the highest mountains.

6. *European endemic species*: *A. frigida*.

Andreaeae are pioneers, and given their wide ecological tolerances they are probably well adapted to survive many types of climatic change, in microniches. So it is not surprising that they survive in small, isolated populations, but the nature of some of the disjunctions is puzzling. Why is *A. rothii* ssp. *falcata* absent from eastern North

America when ssp. rothii is common there and both taxa are sympatric in Europe? Since suitable habitats are plentiful, and A. alpina occurs in the northern part of South America and is from there disjunct to southern Greenland and northwestern Europe, why is it unknown in North America? Do bipolar Andreaeae demonstrate the reverse of the usual pattern of dispersal, from the Northern to the Southern Hemisphere, and if so, how have they become distributed?

In the British Isles, the distribution of Andreaea is linked to ecological factors already discussed. None of the species occurs in southeastern England where the climate is drier, elevations lower and substrates more calcareous than suitable for Andreaea. Table VI-1 shows the distribution of Andreaea species by elevation type. All eleven species occur in Scotland where the greatest diversity of suitable habitats occurs and where the highest elevations and latitudes permit alpine or snow-bed species to exist: A. blyttii, A. crassinervia, and A. sinuosa. Other alpine species occur outside Scotland very rarely and only on high mountains in North Wales: Andreaea nivalis and A. alpestris; or in northern England: A. frigida. More or less widespread in suitable habitats throughout the British Isles are: A. rothii, A. rupestris, and A. alpina. The recently described A. megistospora appears to occur most often in hyperoceanic regions (Chapter IV). A. mutabilis, previously known only from the Southern Hemisphere, has a primarily alpine distribution in the British Isles, but it seems to be quite widespread and tolerant of a wide range of moisture and elevation. None of the alpine species are recorded for Ireland, nor is the bipolar and primarily alpine A. mutabilis.

The three most widespread species, A. rothii, A. alpina, and A. rupestris, are also the most common, accounting for about 85 percent of the total specimens seen. Andreaea alpina and A. rupestris are much more common in Scotland than elsewhere, but A. rothii, characteristically distributed at lower elevations, is more or less evenly distributed throughout the British Isles. The remaining species are rare to very rare and are mostly restricted to alpine areas, especially snowbeds and snow-flushes which are of limited extent in the British Isles.

Classification

The class Andreaeopsida consists of two orders: Andreaeobryales and Andreaeales. I have discussed the characteristics of these groups in Chapter II. The Andreaeobryales, which is represented by just one species, Andreaeobryum macrosporum Steere & B. Murr., is not known outside northwestern North America. The Andreaeales consists of one genus, Andreaea Hedw., of probably fewer than fifty species worldwide.

Since the genus has not been recently, and never thoroughly, monographed and since complete accounts are of costate taxa only (Schultze-Motel 1970) or are out-of-date (Roth 1903-1904, 1910-1911), infrageneric and sectional boundaries are in flux. Based on present understanding, the infrageneric classification of Andreaea in the British Isles is given in Table VI-2.

Subgenus Chasmocalyx has been defined as consisting of species with large but undifferentiated, non-tubular perichaetial bracts. Further study is required, but I have seen differentiated and sheathing perichaetia in some of the Southern Hemisphere taxa. Other features appear to be characteristic of the group: auriculate leaves; a tendency toward partially recurved leaf margins; the occasional occurrence of red leaf bases; small, thin-walled, delicate cells; and a pseudopodium formed from stem as well as archegonial tissue, which can bear tiny bracteoles and axillary hairs well up on its surface. It is possible that _A_. _nitida_ Hook. f. & Wils., presently segregated in its own section (Schultze-Motel 1970), and _A_. _fuegiana_ (Card.) Greene, not treated as a costate species by Schultze-Motel (1970), may fit into subg. _Chasmocalyx_. Only one of the four species currently recognized in this subgenus occurs in Britain.

Subgenus _Andreaea_ includes taxa in which the perichaetial bracts are convolute. It is a heterogeneous group that probably can be divided into several sections. The most common division is into two sections representing costate and ecostate taxa. Costate taxa sort out quite well in sect. _Nerviae_, members of which have been characterized by the presence of a nerve. I have found that species in the section also tend to have persistent axillary hairs, sinuose cell walls, and spores that tend to persist as tetrads for a shorter period than in other taxa and that abort infrequently. Section _Nerviae_ is well represented in the British Isles, with five of the eight known species present.

It is premature to classify the ecostate taxa, since more study is needed; for the present this heterogeneous group is unnaturally combined in sect. _Andreaea_. It appears to me to consist of several distinct lines, some of which may be related to costate taxa (Murray 1987).

I have taken a pragmatic approach toward ranking taxa, since the inherent but different types of variability in the group, the lack of experimental propagation, and the geographic incompleteness of the study lead to uncertainty. Included in this regional treatment are two taxa, A. rupestris and A. alpestris, that are treated as closely related species. They are weakly defined morphologically but distinct ecologically and, in part, also geographically, and they are usually easily recognized in the field. I chose specific rank, since I want to emphasize their distinctive ecological and reproductive characteristics. Andreaea alpestris often occurs on lithosols in large sterile mats, while A. rupestris is typically seen with sporophytes forming small cushions on rock.

I am, at least for the present, using two infraspecific levels, primarily to keep options open, since there are several polymorphic taxa, from other regions, in which grouping within subspecies may be useful. In the case of Andreaea rothii ssp. rothii and ssp. falcata, the subspecific rank was chosen to emphasize the feature that unites the taxa, spore size, rather than the suite of morphological differences that are found in their leaves. These same leaf characteristics occur throughout the genus Andreaea in various forms and combinations, and I am not sure of their systematic significance. Although ssp. rothii and ssp. falcata are morphologically more distinct than A. rupestris and A. alpestris, and they often grow sympatrically, even in the same habitat, in one part of their range (Europe) but allopatrically elsewhere (North America), I have decided against specific ranking. The same situation applies to A. megistospora ssp. megistospora and its North American subspecies, ssp. epapillosa. Rather than recognize four distinct species, I have stressed the factor that ties them together (spore size) and their geographic integrity by using the rank of subspecies (Chapter IV).

Finally, I have used the varietal level to stress the common expressions of apparently clinal variation in the polymorphic species *A. rupestris*. I have not formally recognized most of the variants of *A. rupestris*. However, var. *papillosa*, although intergrading throughout its range with var. *rupestris*, is, in the Arctic, very distinct and merits formal segregation from the rest of the species (Chapter V).

Phylogeny

Since this is a regional treatment, which does not include all taxa within the included subgenera, and since I have not completed monographic study, the phylogenetic relationships of the taxa of the British Isles have not been assessed in detail. The arrangement of the taxa reflects my working hypothesis as to relationships, and a synopsis of major trends at the infrageneric level may be useful here.

I have discussed in Chapter II the phylogenetic relationships of the Andreaeopsida and the included orders, Andreaeobryales and Andreaeales. The Andreaeobryales is the sister group to the Andreaeales and therefore the outgroup to infrageneric taxa of *Andreaea* (the only genus in the Andreaeales). Since the Andreaeobryales consists of only one species, *Andreaeobryum macrosporum*, it must be kept in mind that its features are necessarily (but dangerously) heavily weighted in trying to assess trends within the genus *Andreaea*. By comparison with features in *Andreaeobryum* (see Chapter II), it seems likely that a costa, undifferentiated perichaetial bracts, and dioicous sexuality (as found members of subg. *Chasmocalyx*) are plesiomorphic features and that within subg. *Andreaea*, ecostate taxa demonstrate a derived condition. Occurrence in wet habitats and medium-sized spores are universal in subg. *Chasmocalyx*, so species with large spores in drier habitats (*A. rothii* and *A. megistospora*) show derived states of these characters. The dioicous, small-spored *A. blyttii* is problematic in placement. Since spore abortion is frequent in *Andreaeobryum* and most *Andreaeae*, except members of sect. *Nerviae*, this may be the plesiomorphic condition.

Taxonomy

Andreaea Hedw., *Sp. Musc. Frond.* 47. 1801. Type: *A. rupestris* Hedw.

Plants small to large and robust, caespitose, perennial, darkly pigmented, green only when young or shaded, lipid-filled. Globose multicellular protonemata formed within stretched spore wall, from which branched, rhizomatic, cylindric protonemata and filamentous rhizoids are produced. Small leaf-like protonemal appendages observed in several species. Rhizoids basal on stems and sometimes branches, usually both uni- and bi-seriate. Stems from 0.5 to 10 or more cm long, irregularly branched, often by innovations; in transverse section usually round, usually of ± uniform thick-walled cells, outer cortical cells sometimes smaller and thicker walled than inner, central strand absent. Axillary hairs present, with 1-3(-4) quadrate, brown basal cells and 1(-2-more in inflorescences) cylindrical or clavate, ephemeral or persistent, hyaline or brown when persistent, mucilaginous cells. Primary leaves (irregularly shaped leaves or filaments occurring primarily at bases of stems and branches, resembling protonemal appendages of Andreaea and the pseudoparaphyllia of pleurocarpous mosses) present. Juvenile leaves (minute, imbricate, scale-like leaves) occur frequently along lower portions of stems and branches; concave, usually ecostate even in costate species. Mature leaves spirally arranged, usually evenly and ± densely positioned, larger and denser on upper portions of stems, variable in orientation and shape: in ecostate species lanceolate or panduriform, symmetric or asymmetric, usually clasping below, ± spreading above, and ± constricted, like a waist, near mid-leaf; in costate species usually contracted from sheathing base to the limb; apices often falcate-secund; bases usually somewhat narrowed to a straight insertion; margins usually plane to somewhat incurved, rarely reflexed. Costa present or absent, variable: single or rarely branched, distinctly or indistinctly delineated, short to excurrent, broad or narrow, strong throughout or more rarely lacking apically or basally; in transverse section of ± uniform, thick-walled cells. Laminal cells variable: in ecostate species usually short above, becoming rectangular to elongate below; in costate species often short throughout, some subcostal basal cells rectangular and often yellow; laminal cells usually unistratose in ecostate species, usually bi- to tri-stratose locally in costate species; transverse walls very thin, longitudinal walls often thick and pitted, sometimes thin; walls smooth or sinuose, dorsally papillose or epapillose. Usually cladautoicous, often difficult to demonstrate due to brittle stems; rarely dioicous or gonioautoicous. Perigonia terminal or lateral, gemmate, sessile, inner bracts ecostate, often with crenate margins; antheridia usually 4-10, elliptic, on biseriate stalks; paraphyses numerous or few. Perichaetia terminal, bracts large, often differentiated, convolute and sheathing, innermost usually ecostate in costate species; archegonia terminal or lateral, usually 3-6; paraphyses lacking or few. Pseudopodium usually slender, pale brown to black, slightly twisted to the left in surface view. Sporophytes terminal. Seta absent, sporophyte consists of capsule and bulbous to shortly tapering foot. Capsule usually exserted at maturity, erect, when wet elliptic and valves closed, when dry contracted in length and valves bulging; about 0.5-2.0 mm long; dehiscence by 4(-rarely 6-10) longitudinal, darkly pigmented valves that reach neither base nor apex of capsule, margins of valves ± reflexed when dry, plane to inrolled when wet; paler base from (1/8-)1/4-1/2(-over 3/4) the length of the capsule; neck very short, apex usually shortly conic-apiculate. Exothecial cells rectangular to long-rectangular, sutures consisting of thin-walled cells present; valve exothecial cells with thick longitudinal and thin transverse walls, lumens usually oval, all walls thick in transverse section, inner walls secondarily thickened and darkly pigmented. Stomata absent. Annulus, operculum and peristome absent. Sporogenous tissue and columella derived from endothecium; spore sac dome-shaped, overarching rod-like persistent columella; spore sac not separated by air spaces from capsule walls. Spore abortion frequent to rare, germination endosporic and precocious; spores spherical to angled, small to very large, (10-)13-60(-110) µm, usually finely papillose to reticulate-papillose, rarely almost smooth, often in tetrads until maturity. Spores mature from spring to fall. Calyptra apical, very small, consisting chiefly of unmodified archegonial neck, campanulate-mitrate, persistent or not.

Key to British and Irish Andreaeae

1. Leaves costate 2
1. Leaves ecostate 8
2. Leaf margins crenate to serrate throughout, with sharp laminal and costal papillae. Perichaetial bracts shaped like vegetative leaves .... 1. A. nivalis
2. Leaf margins entire or very rarely dentate above, laminal papillae absent, low costal papillae often present. Perichaetial bracts differentiated, convolute 3
3. Spores (10-)11-19(-23) µm. Basal laminal cells mostly rectangular, walls little pitted, rarely clearly sinuose. Dioicous .... 2. A. blyttii
3. Spores larger than 20 µm. Basal laminal cells mostly quadrate, round, or oblate, sometimes rectangular near costa or margins, walls often strongly pitted and sinuose. Autoicous 4
4. Most spores smaller than 35 µm. Alpine (mostly above 900 m) ... 5
4. Most spores larger than 35 µm. Predominately in lowlands, rarely above 900 m 6

5. Lamina indistinct in upper part of leaf, costa often filling subula, not bulging dorsally. Limb ± abruptly formed .... 3. _A_. _crassinervia_

5. Lamina distinct in upper part of leaf, costa occasionally filling upper part of subula, costa biconvex or bulging. Leaves lanceolate or limb gradually formed .... 4. _A_. _frigida_

6. Spores(30-)35-50(-rarely larger than 60) μm 7

6. Spores (40-)50-90(-110) μm .... 6. _A_. _megistospora_ ssp. _megistospora_

7. Inner perichaetial leaves epapillose or with very low, sparse papillae. Lamina usually distinct to near apex, costa sometimes filling uppermost part of leaf. Leaves usually weakly falcate, rarely brittle; margins entire or with strongly bulging marginal cells .... 5a. _A_. _rothii_ ssp. _rothii_

7. Inner perichaetial leaves papillose above, papillae high and dense. Costa usually filling upper leaf or rarely lamina distinct to near apex. Leaves usually strongly falcate and brittle; margins entire or rarely distantly dentate above .... 5b. _A_. _rothii_ ssp. _falcata_

8. Basal leaf margins denticulate .... 7. _A_. _alpina_

8. Basal leaf margins entire or weakly crenate 9

9. Spores about 13-22 μm 10

9. Spores (16-)24-32(-rarely larger than 40) μm or spores not seen 11

10. Basal marginal cells mostly rectangular. Cell walls strongly pitted and sinuose .... 8. _A_. _sinuosa_

10. Basal marginal cells all quadrate. Cell walls little pitted, never sinuose .... 9. A. mutabilis

11. Basal marginal cells all quadrate .... 9. A. mutabilis

11. Basal marginal cells mostly rectangular, occasionally some quadrate 12

12. Leaves narrowly lanceolate. Cell walls strongly pitted and sinuose .... 8. A. sinuosa

12. Leaves lanceolate or panduriform. Cell walls strongly or weakly pitted, not sinuose 13

13. Leaves usually curved to secund, with oblique apices. Papillae usually prominent and whitish, at least dorsally on upper leaves. Upper cell lumens often stellate, rounded or oval; walls usually incrassate, pitted, and collenchymatous. Plants green-bronze, black or reddish 14

13. Leaves usually straight, apices occasionally oblique. Papillae usually low or absent, very rarely prominent or whitish. Upper cell lumens rounded or stellate; walls incrassate, pitted, and collenchymatous or not. Plants characteristically brown, black, or reddish black 15

14. Leaves lanceolate or occasionally panduriform, gradually narrowed to short or long, obtuse or acute apices .... 10a. A. rupestris var. rupestris

14. Leaves abruptly narrowed from ovate or panduriform bases to long acute apices .... 10b. A. rupestris var. papillosa

15. Leaves ± lanceolate, broadest below mid-leaf, not apiculate. Papillae inconspicuous. Basal cells short-rectangular; lumina broad and bulging, walls little pitted. Upper lamina unistratose

or some leaves with bistratose patches; cell lumens rounded, walls not very collenchymatous or incrassate. Plants black or brown, occasionally reddish black .... 11. A. alpestris

15. Leaves panduriform, broadest above mid-leaf, ± apiculate. Papillae rarely conspicuous. Basal cells rectangular to long-rectangular; lumina rarely bulging, walls pitted. Upper lamina unistratose; cell lumens stellate, walls collenchymatous and incrassate. Plants usually reddish or purple-black, occasionally black. When submerged in running water, greenish and with large, distant, often secund leaves (= A. hartmannii) .... [A. obovata]

1. Andreaea nivalis Hook. (Fig. VI-1)

Trans. Linn. Soc. London 10: 395, Pl. 31, fig. 4. 1811. - Type: Scotland: Ben Nevis, 1808, Hooker & Borrer (holotype: BM-Hooker!; isotypes: BM!).

A. nivalis Hook. var. fuscescens Hook., Trans. Linn. Soc. London 10: 395. 1811. Type: Scotland: Ben Nevis, 1808, Hooker & Borrer (BM-Hooker!, BM!).

Plants medium-sized to very large and robust, brownish green to red-brown. Protonemal appendages not seen. Stems (1-)4-6(-10) cm high; in transverse section often ridged, with several rows of very small outer cells. Axillary hairs with very inconspicuous, small, hyaline, ephemeral mucilaginous cells. Juvenile leaves denticulate. Mature leaves when wet spreading or secund, when dry erect to falcate-secund, distant on lower stems, 1-2 mm long, lanceolate, gradually narrowed from an oblong base to an acute apex; leaf insertion rounded, somewhat decurrent to auriculate; margins irregularly denticulate or crenate from papillose cells, sometimes partially strongly incurved or recurved. Costa present, single (occasional "Siamese twin" leaves with two costae or branched costae and lobed apices seen), subpercurrent or filling leaf apices, distinctly delineated, reddish, strongly papillose dorsally, strongly bulging dorsally, flat ventrally, usually 4-layered, about 1/5 to 1/4 the width of leaf bases, basal cells not sinuose. Lamina distinct in limb, unistratose, or with bistratose patches, areolation distinct, many cells papillose dorsally and ventrally. Laminal cells ± uniform, quadrate to rounded, 8-11 µm, occasionally short-rectangular and often narrower in leaf bases, thin-walled, not pitted, not collenchymatous. Dioicous. Perigonia large and broadly gemmate, paraphyses numerous. Perichaetial bracts similar to mature leaves, but larger, not sheathing or convolute. Capsules occasional, ± globose when dry and dehisced, usually with 4 large and 2 small valves that extend to near bases and apices of capsules, medium-sized to large, 1-1.3 mm long. Spore abortion occasional; spores medium-sized, shrivelled spores 18-22 µm, turgid spores 24-33(-40) µm.

Ecology. On wet acidic rocks (granite, andesite) at edges of streams and flushes that are usually fed by snow-beds; also often forming large mats on seeping outcrops and ledges that are flat to gently sloping. Usually on mountain summits from about 880-1300 m (one collection from 702 m). Very rarely associated with other Andreaeae: A. frigida, A. rupestris, and A. mutabilis.

Distribution. Rare but locally abundant judging by the numerous collections seen from the Ben MacDhui area (v.-c. 94), the Cairngorms (v.-c. 96), and especially the type locality, Ben Nevis (v.-c. 97). I have seen material from all eight vice-counties recorded for *A. nivalis* by Corley & Hill (1981) as well as from Mid Perthshire and, new to Wales, from Caernarvonshire.

Generally found in alpine regions in oceanic parts of the Northern Hemisphere: Europe, Novaya Zemlya, the Caucasus, Asiatic U.S.S.R., Kamchatka, Japan, northwestern and northeastern North America, and Greenland.

Specimens studied (*Ca*. 200). WALES: Caernarvonshire, v.-c. 49: Near Llanberis, no date, *Baker s.n.* (BM-Hunt). SCOTLAND: Mid Perthshire, v.-c. 88: Ben Lawers, Sep 1830, *McIvor s.n.* (DBN); Ptarmigan Hill [?Meall nan Tarmachan], 1830 *s. col.* (E). Angus, v.-c. 90 (1, BM); South Aberdeenshire, v.-c. 92 (4; BM, E); Banffshire, v.-c. 94 (28; ALA, ALTA, BM, DBN, E, NMW); Easterness, v.-c. 96 (28; ALA, BM, DBN, DUKE, E, NMW, herb. Perry); Westerness, v.-c. 97 (121; ALA, ALTA, BBSUK, BM, DBN, DUKE, E, MO, NMW, UBC); Main Argyll, v.-c. 98 (7; BM, E, NMW); West Ross, v.-c. 105 (1, BBSUK); East Ross, v.-c. 106 (1, BBSUK).

Differentiation and Relationships. Easily recognized (when sterile) by its strongly falcate, dense upper leaves, and the rust-brown, strong costa distinctly delineated from the greenish lamina. The only *Andreaea* species with which *A. nivalis* might be confused in the field is *A. frigida*, another mountain plant of wet sites with lanceolate leaves, a strong costa, distinct lamina, and sometimes with a similar color. A close look reveals the diagnostic features of *A. nivalis*: its sharply denticulate and papillose leaves and, when fruiting, the perichaetial bracts that are similar in shape to vegetative leaves and are not convolute.

Andreaea nivalis is the only member of the small, largely Southern Hemisphere subgenus *Chasmocalyx* in the British Isles, so it has no close relatives there.

2. *Andreaea blyttii* Schimp. (Fig. VI-2)

In Bruch, Schimper & Gümbel, *Bryol*. *Eur*. 6: 155, pl. 13(635). 1855. - Type: Norway: "Renöe finmarkiae", 1844, *Blytt* (BM-ex K!, CANM!).

Plants small (in the British Isles) to medium-sized, brown to black, bases often brown and apices black. Protonemal appendages seen. Stems 0.5-2.5 cm high. Axillary hairs with brown, persistent mucilaginous cells. Juvenile leaves apiculate, ± entire. Mature leaves when wet erect-spreading to secund or spreading, when dry erect to secund, brittle; 1-2 mm long; subula ± abruptly formed from a narrow oblong or ovate base, subula 3-4 times longer than the base, narrow, often only 2 cells wide apically, uneven in outline, somewhat fragile. Costa present, single, ± filling subula, weaker or occasionally absent basally, indistinctly delineated, with occasional dorsal papillae, not bulging dorsally, ± terete, of up to 4 (rarely more) layers apically, bistratose or rarely lacking basally, about 1/6 to 1/3 the width of leaf base, basal cell walls rarely sinuose. Lamina indistinct in limb, unistratose or bistratose especially near costa, basally mostly unistratose. Upper laminal cells round or quadrate, (9-)10-12 µm, ± thin-walled, ± smooth to bulging, papillae rare and low. Basal laminal cells rectangular to short-rectangular, in longitudinal rows, walls incrassate, little pitted, very rarely inconspicuously finely sinuose, often with joint thickenings especially conspicuous in transverse section. Basal marginal cells mostly short-rectangular, occasionally a few quadrate, never oblate. Dioicous. Perigonia small, narrowly gemmate, paraphyses occasional to numerous. Perichaetial bracts differentiated, sheathing and convolute, inner bracts ecostate, papillae absent or low and scattered. Capsules occasional, small, about 0.5 mm long. Spore abortion infrequent; spores small, (11-)13-19(-23) µm, almost smooth, green-black to brown.

Ecology. A species of extreme snow-beds, forming extensive sheets on acidic rock slabs or boulders in scree by late snow patches, *ca*. 990-1100 m. Sometimes associated with the widespread *A*. *rupestris* and another snow-bed species, *A*. *sinuosa*.

Andreaea blyttii is frequently overgrown by lichens that are restricted to late snow patches: *Lecanora leptacina* Sommerf., *Lecidea s*. *l*. (det. B. J. Coppins 1985, reported by Gilbert & Fox (1985) as *Caloplaca nivalis* [Körb.] Th. Fr.), and *Lecidea caesioatra* Schaer., said to occur mainly in snow-beds but occasionally found elsewhere (Gilbert & Fox 1985).

Andreaea blyttii has been described as an extreme acidophile in Svalbard (Elvebakk 1984), and it appears to be one in Scotland also. The extreme snow-bed soils in the Cairngorms, where *A*. *blyttii* is found, have a pH in the range of 4.2-4.4 (Gilbert & Fox 1985).

Distribution. Andreaea blyttii is very rare, since in Britain there is very little high ground where, during most years, snow-beds can persist throughout the summer. Only a few Scottish collections (made since 1983) document the presence of A. blyttii in the British Isles.

Elsewhere, sporadically distributed, chiefly in alpine sites, in the Low Arctic (Europe, U.S.S.R., North America, and Greenland) and in Iceland, Europe (Fennoscandia, Poland), and northern North America. To the states and provinces listed by Schultze-Motel (1970) can be added Oregon, the Yukon, Quebec, and the island of Newfoundland.

Heslop Harrison & Cooke (1942) reported A. blyttii (and A. hartmannii) as new to the British Isles, from the Outer Hebrides. These species were omitted by Richards & Wallace (1950) from their checklist of British mosses "pending confirmation," and Smith (1978) and Corley & Hill (1981) do not include them in the moss flora of the British Isles, since Smith said that the records were not substantiated. Some vascular plant records of Heslop Harrison have been thought to be alien introductions (Raven 1949), and according to D. G. Long (*in litt*. 1984) that is the reason the reports of A. blyttii and A. hartmannii (= A. obovata) are considered doubtful.

In July 1985, I was (I thought) finishing my study of Andreaea in the British Isles. During a brief trip to Britain, I spent a little time studying lichens growing on Andreaeae with B. J. Coppins at the Royal Botanic Garden, Edinburgh. I was very surprised to see material of A. blyttii (collected incidently by O. L. Gilbert during a study of lichen vegetation in snow-beds on Cairn Gorm) in the Lichen Herbarium at E, since I had seen none in bryophyte herbaria except the doubtful material just mentioned. Brian Coppins kindly searched through other collections of snow-bed lichens for *Andreaea* material, and I was soon even more surprised (and delighted) to see, in several of his collections from Beinn Dearg, material of a new species (*A. sinuosa*) that I was in the process of describing from Alaska and British Columbia. Since snow-beds in Britain have been little studied by bryologists, David Long and I changed our plans for upcoming field work in favor of a snow-bed site. Within a few minutes of reaching S Top on Beinn a'Bhuird, we found both *A. blyttii* (in abundance) and *A. sinuosa* (a few stems) on boulders in scree immediately adjacent to a snow-patch. Another species rarely collected in Britain, *A. alpestris*, was abundant on lithosols just below the snow-patch.

In 1986, David Long re-visited Beinn Dearg, while leading the BBS summer field meeting, and found *A. blyttii*, in abundance, as well as *A. sinuosa* and *A. alpestris*. It is likely that serious study of snow-beds by bryologists will be as rewarding as it has proved to be for lichenologists (Gilbert & Fox 1985).

Specimens studied (7). SCOTLAND: South Aberdeenshire, v.-c. 92, S Top, Beinn a'Bhuird, grid reference 37/095977, 13 Jul 1985, *Murray & Long s.n.* (ALA, E, replicates to be distributed in an exsiccata of *Andreaea* in preparation), *Long & Murray 12791* (E). Easterness, v.-c. 96, Margaret's Coffin, Cairngorm, 38/011047, Aug 1983, *Gilbert s.n.* (E). West Ross, v.-c. 105, Beinn Dearg, N slope, 28/259815, *Long 13790* (E). East Ross, v.-c. 106, Beinn Dearg, NE slope, 28/261814, *Long 13798* (ALA, E).

Specimens seen, reported by Heslop Harrison & Cooke (1942). SCOTLAND: Outer Hebrides, v.-c. 110: Harris: Sron an Toister, Jul 1941, J. W. Heslop Harrison (BM, E, NMW, herb. Wallace); Toddun, Aug 1941, Clark (E).

Differentiation and Relationships. The only other costate Andreaea species that occurs in snow-beds is the very distinctive A. nivalis. In color and size alone, the two are distinct: A. blyttii small and black, A. nivalis quite large and green-brown to red-brown. In Scotland the two species evidently grow in somewhat different habitats, since they have not been found associated. Andreaea blyttii occurs in extreme snow-bed conditions on rocks that are under snow early in the season and exposed and dry during the short growing season. Andreaea nivalis is found in wet flushes and streams that issue from snow-beds or on seeping ledges.

Andreaea blyttii differs most obviously from other members of sect. Nerviae by its very narrow subula, often only two cells wide above. In addition, it is dioicous, the basal cells are mostly rectangular, the costa is often weak to absent basally, and the spores are small (13-19 μm). Some plants can look superficially like A. crassinervia, which has, however, short marginal basal cells and larger spores. See Table VI-3 for a comparison of diagnostic features of members of sect. Nerviae in the British Isles.

The only other species in the section with rectangular marginal basal cells and a weak costa has not been recorded in the British Isles. Andreaea heinemannii Hampe & C. Müll. (= A. angustata Lindb. ex Limpr.) is known from continental Europe, and there is no reason it should not be found in the British Isles. It differs from *A. blyttii* by its autoicous condition, larger spores (25-32 µm), and leaves often with strongly sinuose basal cell walls.

Andreaea blyttii stands apart from other members of sect. *Nerviae* by its dioicous condition, small, almost smooth spores, and only slight tendency toward sinuose basal cell walls.

3. *Andreaea crassinervia* Bruch (Fig. VI-3)

Abh. Math.-Phys. Classe Koen. Bayer. Akad. Wiss. 1: 279, *10*. 1832. *A. rothii* Web. & Mohr ssp. *crassinervia* (Bruch) Dix., *Stud. Handb. Brit. Mosses* 27. 1896. Type: Switzerland, Grimsel, *Maerker* (BM-Bruch in Herb. Schimper!)

Plants small to medium-sized, brown to black. Protonemal appendages not seen. Stems 0.5-2.5 cm high. Axillary hairs with brown, persistent mucilaginous cells. Juvenile leaves apiculate, sometimes sparsely toothed from projecting cells. Mature leaves when wet erect-spreading to secund, when dry erect to falcate-secund; 1-2 mm long, ± abruptly tapering from an ovate base to an acute subula that is 2 to 4 times as long as the leaf base. Costa present, single, excurrent and filling almost entire subula, strong, indistinctly delineated, often papillose, costa not bulging dorsally, of up to 6(-7) layers apically, weaker basally, usually over 1/3 to 1/2 the width of leaf base; basal costal and subcostal cells walls often sinuose. Lamina indistinct and usually present only in lower 1/3 of limb, uni- to tri-stratose locally, basally mostly unistratose. Upper leaf cells round, oval or oblate, 9-12 µm, thin-walled, smooth to bulging. Basal laminal cells similar to upper, rectangular only near costa. Cladautoicous and gonioautoicous. Perigonia small, narrowly gemmate, paraphyses numerous. Perichaetial bracts differentiated, convolute and sheathing, inner bracts ecostate, papillose or epapillose, papillae usually scattered, low and rounded, rarely dense or sharp and oblique. Capsules common, medium-sized, about 1 mm long. Spore abortion infrequent, spores medium-sized, (20-)26-36(-40-50) µm.

Ecology. Unknown in Britain. Usually alpine, in the Alps indicative of continuously trickling water (Geissler 1982). In eastern North America, it occurs also at low elevations.

Distribution. Very rare. I have seen only one collection of A. crassinervia from the British Isles.

Primarily an alpine species, known from Europe and northeastern North America as far west as the Great Lakes region. To the regions cited by Schultze-Motel (1970) can be add Germany, Quebec, Ontario, and Michigan. I have not been able to verify the occurrence of A. crassinervia in arctic Canada or Greenland (Chapter V).

Material previously cited as A. crassinervia from Britain was misidentified. I have examined material of all the specimens cited by Lindberg (1870), all but one of those cited by Braithwaite (1880-1887), including the one illustrated (Hebden Bridge, Hunt), and the three cited by Schultze-Motel (1970). I have determined them to be A. rothii ssp. falcata. I have not seen the collection from Falcon Clints, Teesdale, 1853, Slater, cited by Braithwaite, but have seen many collections of A. rothii ssp. falcata from that locality and none of A.

crassinervia. *Andreaea crassinervia* was reported from 32 vice-counties by Smith (1978) and from 20 vice-counties by Corley & Hill (1981), but I have seen no material of the species from any of them.

The single collection seen (apparently not previously reported) was in NY and had a piece of paper glued to the packet, as a label, with handwriting in pencil: "more than half of all I have *no fr* Andrea crassinervia Dhuloch Aberdeenshire Rev. ?J[illegible] F 18?0[illegible]." Other labels (in the same hand) of gatherings of other species at NY spell out Rev. J. Ferguson and give 1890 as the year of collection. There is however a neatly labelled specimen in H-Brotherus of *A. alpina* from Dhuloch collected by J. Ferguson in May 1870, so perhaps that is the year of collection. The Rev. John Fergusson (1834-1907) was a Scots minister who studied mosses. I have seen only three specimens of Fergusson material of *Andreaea* in British herbaria. Many of Fergusson's collections were destroyed by fire (Duncan 1966), so it is of interest to know that there are duplicates in NY and H.

Since *A. crassinervia* is vouched for in Britain only by one scanty, evidently divided, poorly labelled specimen, it should be sought again in the Dhu Loch area. David Long localized the collection.

Specimen studied. SCOTLAND: Aberdeenshire, v.-c. 92, Dhu Loch, near Lochnagar, probably the NE facing cliffs, grid reference 37/2382, ?1870, *Fergusson* (NY).

Differentiation and Relationships. *Andreaea crassinervia* is easily recognized by its leaves with a very wide costa that fills almost the entire subula. The costa is not distinctly delimited from the lamina in the lower subula, and it is not dorsally convex; instead the lamina and costa form a continuous arc in transverse section (Fig. VI-3g). Compare with the dorsally bulging costa of *A. rothii* (Fig. VI-6e). *Andreaea crassinervia* is further distinguished from other species in which the costa fills a large part of the subula, by its spores, which are larger than those of *A. blyttii* and smaller than those of *A. rothii* ssp. *falcata*. See Table VI-3.

Andreaea crassinervia has often been included in *A. rothii*. However, it stands apart on account of its smaller spores and very wide costa. By its medium-sized spores and alpine distribution in wet habitats, *A. crassinervia* seems more closely related to *A. frigida* than to *A. rothii*.

Most of the difficulty that has been caused by this species in Britain and Ireland, is attributable to the fact that British bryologists have been studying material of *A. rothii* ssp. *falcata* and trying, without possibility of success, or becoming frustrated in trying, to fit it into *A. crassinervia* (see the perceptive discussion by Dixon in Dixon & Jameson 1924). The long-standing taxonomic confusion is further discussed under *A. rothii* ssp. *falcata*.

4. *Andreaea frigida* Hüb. (Fig. VI-4)

Hep. Germ. 305. 1834. *A. rothii* Web. & Mohr var. *frigida* (Hüb.) Lindb. *in* Braithw., *Brit. Moss-Fl.* 1: 13. 1880. *A. rothii* Web. & Mohr ssp. *frigida* (Hüb.) Schultze-Motel, *Herzogia* 1: 69. 1968. Type:

Switzerland: Grimsel, Schaerer. Neotype: Switzerland, Grimsel, Schimper (B!), chosen by Schultze-Motel (1970).

Plants large, red-brown. Protonemal appendages not seen. Stems to over 4 cm high. Axillary hairs with brown, persistent mucilaginous cells. Juvenile leaves tiny, rarely seen. Mature leaves when wet erect, straight sometimes secund, when dry little changed; 1-2.3 mm long, ± lanceolate or gradually narrowed from ovate base to acute limb that is 1 1/2 to 2 times as long as the leaf base. Costa present, single, percurrent to rarely excurrent and filling upper 1/4 of limb, ± distinctly delineated, smooth, biconvex or bulging dorsally, of up to 6(-7) layers apically, weaker basally, about 1/4 to 1/3 the width of leaf base; basal costal and subcostal cell walls often clearly sinuose. Lamina distinct in limb, often bistratose or with bi- and uni-stratose areas, mostly unistratose basally. Upper laminal cells round, oval or oblate, 8-12 µm, ± thin-walled, smooth to bulging. Basal laminal cells similar to upper, rectangular only near costa. Cladautoicous. Perigonia large, broadly gemmate, paraphyses numerous. Perichaetial bracts differentiated, sheathing and convolute, inner bracts partly costate, rarely ecostate, papillae absent. Capsules frequent (present in all British material), large, up to 1.6 mm long. Spore abortion infrequent, spores medium-sized, (20-)25-35(-40) µm.

Ecology. On wet acidic rocks in mountain streams or on ridges. Reported on rocks in stream near summit of Ben MacDhui (Braithwaite 1880-1887). A note by A. Croall on one of his specimens at BM reported that A. frigida was only on the west side near the summit (1220 m), confined to ridge rocks of Ben MacDhui forming Glen Dee and opposite Cairn Toul and Putnam Pouch. One specimen included *A. nivalis*.

Distribution. Very rare. I have seen material from two of the vice-counties reported by Corley & Hill (1981) and have added a record from North-west Yorkshire. All collections but one from Cumberland were made in the 1800s. The source of the records from Easterness and Westerness (Corley & Hill 1981) is not known (M. O. Hill *in litt.* 1985).

A European (including the British Isles) endemic. Portugal can be added to the countries cited by Schultze-Motel (1970).

Specimens studied (13). ENGLAND: North-west Yorkshire, v.-c. 65: Cronkley Scars, Teesdale, grid reference 35/8429, Sep 1854, *Black* (BM). Cumberland, v.-c. 70 (1, BBSUK). SCOTLAND: South Aberdeenshire, v.-c. 92 (11; BM, E, H, NY).

Differentiation and Relationships. Recognizable by the combination of gradually narrowed, lanceolate leaves with the lamina distinct to the apex and medium-sized spores. Easily distinguished from *A. rothii* and *A. megistospora* also by its large size and occurrence in wet alpine habitats and from *A. nivalis* by its entire, epapillose leaves and convolute perichaetial bracts.

Probably most closely related to the recently described, western North American endemic species, *A. schofieldiana* B. Murr. (Chapter IV), with which it shares the lanceolate leaf shape and medium-sized spores. *Andreaea frigida* was treated as a subspecies of *A. rothii* by Schultze-

Motel (1970), who considered the most important character to be the lamina-costa relationship in the upper part of the leaf. In my opinion, spore size is the most important feature defining taxa in sect. Nerviae, and by this criterion A. frigida is more closely related to A. crassinervia, for example, than to A. rothii. See Table VI-3. It is of interest that medium-sized spores are found in the taxa in sect. Nerviae with alpine rather than subalpine distribution. It is possible that two lines, one with medium-sized spores, the other with large spores evolved from stocks with these two habitat preferences.

Because of its lanceolate leaf, strong costa, and medium-sized spores, I think A. frigida may be one of the more primitive members of sect. Nerviae, having in common several features of subg. Chasmocalyx, which I consider the most primitive group of Andreaeae.

5. Andreaea rothii Web. & Mohr, Bot. Taschenb. 386. 1807. A. rupestris A. Roth, Neue Beitr. Bot. 1: 232. 1802, hom. illeg., non A. rupestris Hedw., 1801. Type: NW Germany, "in cippo sepulcrali ethnicorum in duc. Brem. inter Hagen et Meyenburg", Roth, not seen.

Plants small to medium-sized, brown to black. Protonemal appendages not seen. Stems 0.5-2.5 cm high. Axillary hairs with brown, persistent mucilaginous cells. Juvenile leaves apiculate. Mature leaves when wet erect-spreading to secund, when dry erect to secund; about 1-2 mm long, usually sharply contracted at the shoulder to an acute limb. Costa present, single, percurrent to excurrent and filling upper limb, distinctly delineated, with occasional dorsal papillae, costa bulging dorsally, of up to 6 layers apically, weaker basally, about 1/6 to 1/3 the width of the leaf base; basal cell walls often sinuose. Lamina uni- to partly or completely bi-stratose above, base usually unistratose. Upper laminal cells mostly round to oblate, 8-12 µm, thin-walled, smooth or bulging. Marginal basal laminal cells similar to upper cells, longer towards costa. Cladautoicous and gonioautoicous. Perigonia small, narrowly gemmate, paraphyses numerous. Perichaetial bracts differentiated, convolute and sheathing. Capsules common, medium-sized, about 1 mm long. Spore abortion infrequent, spores large (30-)36-52(-60-80) µm.

5a. Andreaea rothii ssp. rothii (Fig. VI-5)

A. rothii Web. & Mohr var. hamata Lindb. ex Braithw., Brit. Moss-Fl. 1: 13. 1880. Types: Ireland, "Luggielaw, Wicklow (Lindberg 1873). Wet rocks at Carfury, Madron near Penzance (Curnow and Marquand 1879)." Luggielaw, 1873, Lindberg (BM!, NY ex herb. Lindberg!).

Leaves erect to secund, rarely distinctly falcate, not brittle; limb 2 to 3 times as long as the leaf base; lamina distinct in limb; margin of limb entire or crenate from bulging cells. Costa usually percurrent, when excurrent filling only upper 1/4 of limb. Innermost perichaetial bracts usually with trace of costa, epapillose or with very low sparse papillae.

Ecology. On dry to wet rocks from sea level to about 750 m elevation. Because this subspecies has been misunderstood and is uncommon in the British Isles, its habitat requirements are unclear, but apparently are similar to those of ssp. falcata.

Distribution. Occasional to rare. Of about 720 specimens of A. rothii s.l. seen, only about 75, or a little over ten per cent are referable to ssp. rothii.

All material cited by Lindberg (1870) and quite a bit cited by Braithwaite (1880-1887) and Schultze-Motel (1970) is actually ssp. falcata. Subspecies rothii was reported for 101 vice-counties by Corley & Hill (1981), but I have seen material from only about 37 and often only one specimen from a vice-county.

Known also from continental Europe and eastern and western North America. Reported from Mongolia (Abramova & Tsegmed 1979). Reported from the Faroes, but I have only seen material of ssp. falcata from there.

Specimens studied (Ca. 75). ENGLAND: West Cornwall, v.-c. 1 (2; BM, E); East Cornwall, v.-c. 2 (6; BBSUK, BM); South Devon, v.-c. 3 (5; BM. NMW); Shropshire, v.-c. 40 (2; BM, NMW); West Lancashire, v.-c. 60 (3, NMW); South-west Yorkshire, v.-c. 63 (1, BBSUK); Mid-west Yorkshire, v.-c. 64 (1, BM); North-west Yorkshire, v.-c. 65 (1, BBSUK); Westmorland, v.-c. 69 (1, E). ISLE OF MAN, v.-c 71 (2, DBN, NMW). WALES: Glamorgan, v.-c. 41 (2, NMW); Pembrokeshire, v.-c. 45 (1, herb. Perry); Caernarvonshire, v.-c. 49 (2, NMW). SCOTLAND: Kirkudbrightshire, v.-c. 73 (2, E); Selkirkshire, v.-c. 79 (1, E); East Lothian, v.-c. 82 (3, ALA, E); West Perthshire, v.-c. 87 (5, E); Mid Perthshire, v.-c. 88 (1, E); Angus, v.-c. 90 (1, BM); Easterness, v.-c. 96 (1, E);

Main Argyll, v.-c. 98 (1, E); West Ross, v.-c. 105 (3, E); East Ross, v.-c. 106 (1, E). IRELAND: South Kerry, v.-c. H1 (6, BM, DBN); North Kerry, v.-c. 2 (3, BM); East Cork, v.-c. H5 (2, BM, DBN); Limerick, v.-c. H8 (1, BBSUK); Wexford, v.-c. H12 (1, BBSUK); Carlow, v.-c. H13 (1, DBN); West Galway, v.-c. H16 (1, BM); Wicklow, v.-c. H20 (5; BM, DBN, MO, NY); Dublin, v.-c. H21 (1, BM); West Mayo, v.-c. H27 (1, DBN); Cavan, v.-c. H30 (1, BBSUK); West Donegal, v.-c. H35 (1, BM); Tyrone, v.-c. H36 (1, DBN); Down, v.-c. H38 (2; BM, DBN).

Differentiation. See Table VI-3. Throughout most of its range, ssp. *rothii* is quite easily distinguished from ssp. *falcata* by its only slightly secund, non-brittle leaves in which the lamina is usually distinct to the leaf apex, with the costa only occasionally excurrent and filling the uppermost part of the limb. Perichaetial bracts are smooth; only rarely is there a hint of true papillae. In the British Isles, however, a form (described as var. *hamata*) is the most frequent expression of this taxon. It has features that are intermediate to ssp. *falcata*--leaves are sometimes more strongly falcate and the costa more commonly excurrent than in typical material, and low, sporadic papillae are seen in some plants within a population. In the British Isles very few specimens appear to totally lack papillae. Because it is often difficult to determine if papillae are present or not (they only occur in scattered plants), it seems practical to treat this form within ssp. *rothii*, at least until its expression throughout the range of ssp. *rothii* is determined. Based on what I have seen so far, the intermediate form appears to be more frequently expressed in northwestern than in central or southern Europe, and it does not occur in North

America. It is possible that it resulted from hybridization between ssp. *rothii* and ssp. *falcata* and is thus more frequent where ssp. *falcata* is common, but this is only speculation.

Subspecies *rothii* is separable from *A*. *frigida* by its more abruptly formed limb, its larger spores, and its tendency to occur at lower elevations and in drier sites. Subspecies *rothii* has smaller spores than and lacks the dense perichaetial papillae of *A*. *megistospora* spp. *megistospora*.

5b. *Andreaea* *rothii* ssp. *falcata* (Schimp.) Lindb. (Fig. VI-6) *Musc*. *Scand*. 31. 1879. *A*. *falcata* Schimp., in Bruch, Schimper & Gümbel, *Bryol*. *Eur*. 6: 154. pl. 12(634). 1855. *A*. *rothii* Web. & Mohr var. *falcata* (Schimp.) Lindb., in Braithw. *Brit*. *Moss-Fl*. 1: 14. 1880. Types: Switzerland, "Ad rupes graniticas saepe ororatas glaciei moles cingentes quas *Bernina-Gletscher* appellant, in Helvetiae valle *Engadin* (W. Ph. Schper.); e Hercynia superiore cl. Leo Lesquereux retulit." Bernina Gletscher, August 1845, *Schimper* (lectotype chosen here: BM-Schimper!; isolectotypes: BM-Hooker!, BM-Hampe!, BM-Bruch!, BM-Wilson!); Harzburg, Clausthal, 1845, *Lesquereux* (syntypes: BM-Hampe!, BM-Bruch!, NY!)

A. *rothii* var. *papillosa* C. Müll., *Syn*. *Musc*. *Frond*. 1: 9. 1848. Type: "In unica rupe ad Bernina Gletscher Engadin" Aug 1845, *Schimper* (holotype: BM-Hampe!)

A. *huntii* Limpr., *Laubm*. *Deutschl*. 1: 145. *55*. 1885. *A*. *crassinervia* Bruch var. *huntii* (Limpr.) Braithw., *Brit*. *Moss-Fl*. 1 Suppl.: 295.

1887. *A. rothii* Web. & Mohr var. *huntii* (Limpr.) Dix., *Stud. Handb. Brit. Moss.* 27. 1896. *A. rothii* Web. & Mohr ssp. *huntii* (Limpr.) Joerg., *Berg. Mus. Aarb.* 1894-95(13): 13. 1897. *A. crassinervia* Bruch ssp. *huntii* (Limpr.) Amann, *Fl. Mouss. Suisse* 1: 28 and 2: 19. 1919. *A. commutata* Limpr., *Jahresber. Schles. Ges. Vaterl. Cult.* 61: 221. 1883, *hom. illeg. non A. commutata* C. Müll., 1864. Type: Ockerthales in Harz, April 1876, *Bertram* in Bryoth. Eur. 1301 b (lectotype: B!, chosen by Schultze-Motel 1970).

Nomenclature and Taxonomy. *Andreaea rothii* ssp. *falcata* was first recognized in Switzerland in 1845 and given by Bruch and Schimper the name *A. falcata* on herbarium labels. Publication of the name did not soon follow, and, in the interim, C. Müller (1848) published the name *A. rothii* var. *papillosa* for the same taxon giving as the type "*Andr. falcata* Schimp. in Hb. Hampeano....in unica rupe ad 'Bernina Gletscher im Engadin:' W. P. Schimper. Aug. 1846 [*sic*]. Dom. Lesquereux (e litt. *Hampeanis*) in hercynia superiore observavit." Some years later Schimper (Bruch, Schimper & Gümbel 1855) published *A. falcata* and included as a synonym Müller's variety, which, however, Schimper referred to as var. *falcata* C. Müll (not var. *papillosa*).

Müller (1848), who considered the taxon within the range of *A. rothii s. l.*, characterized it as having leaves in which the costa totally filled the apex and in which the apical cells were more papillose and erose-denticulate than in var. *rothii*. Schimper (Bruch, Schimper & Gümbel 1855), on the other hand, compared *A. falcata* to *A. crassinervia*. He distinguished *A. falcata*, among other things, by its more falcate leaves and the erose-emarginate apex with the costa disappearing in or below the apex. He stated, furthermore, that *A*. *falcata* could in no way be confused with *A*. *rothii* (which he called *A*. *rupestris* Turn.) as he felt had been done by Müller. Thus, from the very beginning we had a taxon that was considered related to two different species by two taxonomists and was described as having features intermediate to those considered diagnostic for *A*. *rothii* *s*. *str*. and *A*. *crassinervia*. That is, the costa filled the apex of the leaf more than in *A*. *rothii* *s*. *str*. and less than in *A*. *crassinervia*.

In 1885 Limpricht (1885-1889) named *A*. *huntii* (to replace his later homonym, *A*. *commutata*; see synonymy above). *Andreaea* *huntii* was reported from Germany, Norway, and Scotland. The Scottish plants were collected by G. E. Hunt of Manchester (for whom the species was named). As Limpricht noted, Schimper (1876) had already referred Hunt's British collections to *A*. *falcata*. However, using a new character, the perichaetial bracts, Limpricht recognized *A*. *huntii* as a distinct species differing from others in the group primarily by its inner perichaetial bracts with crenulate margins and large dorsal papillae.

Limpricht stated that he had not been able to ascertain if Schimper's plant had these features, and he used Schimper's original description of *A*. *falcata* to lead him to the conclusion that *A*. *huntii* could not be identified with *A*. *falcata*. It is not clear why Limpricht was not able to determine whether *A*. *falcata* had strongly papillose inner perichaetial bracts, since he cited both syntypes of *A*. *falcata* in his discussion of that taxon in the same publication in which he described *A*. *huntii* (Limpricht 1885-1889).

Limpricht stated that the type material of *A*. *falcata* from Bernina was sterile and appeared to be a stunted form of yet another species, *A. frigida*. Fruiting type material from Harz, collected by Lesquereux, was, however, listed under *A. falcata* (as *A. rothii* var. *falcata*). So the initial taxonomic disagreement of Müller and Schimper was compounded with confusion when Limpricht introduced a new species, *A. huntii*, which he assumed was different from *A. falcata*, although he did not evaluate in *A. falcata* the primary diagnostic feature of *A. huntii*. Limpricht also suggested that the syntypes of *A. falcata* consisted of two taxa, *A. falcata* and *A. frigida*.

In 1880 Braithwaite, in Volume 1 of his *British Moss-flora* (1880-1887), treated *A. falcata* as a variety of *A. rothii* citing Lindberg *in litt*. as the authority for the new combination. When Braithwaite completed the first volume of the *British Moss-flora* in 1887, he included a Supplement in which he treated Limpricht's new (1885) species as a variety of *A. crassinervia* (var. *huntii* [Limpr.] Braithw.). He noted, as had Limpricht, that the specimens cited in *British Moss-flora*, including Hunt's, were regarded as *A. falcata* by Schimper.

From this time on, in Britain (and elsewhere), Schimper's *A. falcata* and Limpricht's *A. huntii* were often treated as separate taxa at various ranks, *A. falcata* closer to *A. rothii s. str*. and *A. huntii* closer to *A. crassinervia* (e.g. Dixon 1896, Dixon & Jameson 1924). Even though he separated the two, Dixon seriously questioned his decision and their distinctness. But, other than Schimper, only Mönkemeyer (1927), Podpera (1954), and Wijk *et al*. (1959, following Podpera), actually treated the two names as synonyms.

Schultze-Motel (1970), who monographed costate *Andreaeae*, treated *A. huntii* as a subspecies of *A. crassinervia*. He regarded *A. falcata* as a *nomen confusum*. He cited Article 69 of the International Code of Botanical Nomenclature (Lanjouw 1966) "A name must be rejected if it is used in different senses and so has become a long-persistent source of error" and Article 70 "A name must be rejected if it is based on a type consisting of two or more entirely discordant elements, unless it is possible to select one of these elements as a satisfactory type." Article 70 was deleted at the Leningrad Congress in 1975 and Article 69 has been revised. However, even as they stood in 1966 (and according to the present Code [Voss 1983]), *A. falcata* is neither a candidate for rejection, nor should there be any nomenclatural confusion.

Schultze-Motel (1970) stated that if one of the syntypes of *A. falcata* (from Bernina) is in fact *A. frigida* (Limpricht 1885-1889), then the lectotype for *A. falcata* must be the other syntype, the collection by Lesquereux from Oberharz. Since Schultze-Motel had not seen the "lectotype" collected by Lesquereux, he suggested that *A. falcata* be treated as a *nomen confusum* until it could be decided if it was synonymous with either *A. rothii* or *A. crassinervia* ssp. *huntii*.

In the list of specimens cited as *A. rothii* ssp. *frigida* (= *A. frigida*) by Schultze-Motel (1970) is one housed in E from Bernina, Engadin, that was collected and named *A. falcata* by Schimper. I have examined this specimen, which is probably part of the type gathering, and concur with Schimper's identification (a little *A. rupestris* is intermixed). I have examined syntypes of *A. falcata* collected by Schimper at Bernina Glacier, Engadin, in August 1845 and by Lesquereux between Clausthal and Harzburg in 1845 from several herbaria including Schimper's in BM. In no instance have I seen mixtures with other costate taxa, and all the material is referable to Schimper's *A.*

falcata. I have also examined other authentic material (from Wales and Scotland), and in all cases Schimper was consistent in his determinations. All represent his *A. falcata*. The types that I have seen do not consist of discordant elements as suggested by Limpricht (1885-1889) and Schultze-Motel (1970).

Since its inception, *A. falcata* has been treated as a species or as an infraspecific category of *A. rothii*. It is really the circumscription of *A. rothii* and *A. crassinervia* and the identity of *A. huntii*, which was named later, that have been confused. None of this confusion is sufficient to permit rejection of any of the names, since their nomenclatural base is clear, and types of all taxa (except *A. rothii* Web. & Mohr) are available. Disagreement has been taxonomic and the confusion is by no means universal. After examining types, I have concluded that *A. falcata* and *A. huntii* are taxonomic synonyms that fall within the range of variation of *A. rothii* *s. l.*, so I have treated the taxon as *A. rothii* ssp. *falcata*.

Leaves usually strongly secund to falcate-secund, brittle, limb 3 to 5 times as long as the leaf base; lamina indistinct or sometimes distinct in limb; limb margin entire, crenate from bulging cells or rarely distantly dentate. Costa usually excurrent and filling upper 1/2 to 1/4 of the subula, occasionally percurrent. Innermost perichaetial bracts usually ecostate, rarely with a trace of costa; papillose above, papillae usually dense, sharp and oblique, sometimes lacking in some plants in a population.

Ecology. On dry to wet acidic rock (granite, sandstone, shale, slate), from near sea level to rarely above 900 m.

Distribution. Common in suitable habitats throughout the British Isles. I have seen material from about 82 vice-counties from southwestern England to the Shetlands and throughout Ireland. Considered very rare and reported (as *A*. *crassinervia* ssp. *huntii*) from five vice-counties by Smith (1978), from 12 vice-counties by Schultze-Motel (1970), and from seven by Corley & Hill (1981), for a total of only 15 vice-counties. The discrepancy is because most material previously identified as ssp. *rothii* or *A*. *crassinervia* ssp. *crassinervia* is in fact ssp. *falcata*.

Outside the British Isles, ssp. *falcata* is known from continental Europe. To places listed by Schultze-Motel (1970) can be added the Faroes, Sweden, Spain, and Sardinia. I have also seen one North American collection referable to ssp. *falcata* (Oregon, Douglas County, *Christy* *488*, herb. Christy, DUKE).

Specimens *studied* (*Ca*. 650; from v.-c. 1-5, 34-37, 41-50, 52, 57, 58, 60, 62-73, 78, 80, 82, 83, 86-92, 94-100, 102-108, 110-112, H1-H3, H5, H6, H10, H16, H20, H21, H25-H31, H33, H35, H38, H39; in ALA, B, BBSUK, BM, DBN, DUKE, E, H, MO, NMW, NY, UBC, UCNW, herb. Perry).

Differentiation. See Table VI-3. Typical material of ssp. *falcata* can be recognized by its strongly falcate leaves with a long excurrent nerve filling the upper subula and by the strongly papillose inner perichaetial bracts. Occasionally material occurs in which papillae are present on some plants within a population but absent in others, and it is sometimes necessary to check more than one perichaetium. Perichaetial papillae can usually be seen if inner perichaetial bracts are exposed under a dissecting scope; rarely is it necessary to use a compound scope with typical material. The small amount of material with features in all ways intermediate to those of ssp. *rothii* is probably best treated as *A. rothii s.l.*

Subspecies *falcata* is easily distinguished from *A. crassinervia* by its larger spores, its lamina that is distinct in the upper part of the leaf (even if only a narrow border is visible), and its dorsally bulging, narrower costa.

6. *Andreaea megistospora* B. Murr. ssp. *megistospora* (Fig. VI-7)
Chapter IV, also submitted for publication. Type: Scotland: Main Argyll, v.-c. 98, Meeting of Three Waters, Pass of Glencoe, 31 October 1982, *Murray & Long s.n.* (holotype: E; isotypes: ALA and others to be distributed in an exsiccata of *Andreaea* in preparation).

Plants small, rarely medium-sized, brown to black. Protonemal appendages rarely seen. Stems usually less than 1 cm high, rarely to 1.5 cm. Axillary hairs with brown, persistent mucilaginous cells. Juvenile leaves about broadly ovate, apiculate. Mature leaves when wet erect-spreading or secund, when dry appressed, 1-2 mm long, often sharply contracted at the shoulder from an ovate or oblong base to an acute limb that is 2 to 3 times as long as the leaf base. Costa present, single, percurrent to excurrent and filling upper 1/4 of the limb, strong, distinctly delineated, with occasional dorsal papillae, costa biconvex or bulging dorsally, of up to 6 layers apically, rarely weaker basally, about 1/6 to 1/4 the width of the leaf base; basal cell walls often sinuose. Lamina distinct in limb, unistratose or partly to completely bistratose, base usually unistratose. Upper laminal cells mostly round to oblate, 8-12 µm, thin-walled, smooth or bulging. Basal laminal cells similar to upper or slightly longer. Cladautoicous and gonioautoicous. Perigonia small, narrowly gemmate. Perichaetial bracts differentiated, convolute and sheathing, inner bracts ecostate, papillose, papillae usually low and rounded, rarely sharp and oblique. Capsules common, small, to about 0.8 mm long. Spore abortion infrequent, spores very large (40)50-90(110) µm.

Ecology. On dry to moist, usually exposed rock, from near sea level to about 700 m (one collection from 1100 m in Scotland). Sometimes associated with widespread taxa, *A. rupestris*, *A. rothii* ssp. *falcata*, and *A. alpina*, rarely with *A. mutabilis*.

Distribution. Rare. Known only from the British Isles, Norway and northwestern North America (Chapter IV). *Andreaea megistospora* is a member of the group of western European-western North American disjuncts that occur in hyperoceanic regions and are probably relict species whose ranges were contracted during the Quaternary (Murray 1986).

Specimens studied (*Ca.* 35, an asterisk [*] represents a specimen, lacking spores, identified by leaf characteristics). ENGLAND: County Durham, v.-c. 66, Falcon Clints, Teesdale, grid reference 35/8228, Sep

1854, *Black* (BM); Cumberland, v.-c. 70, Swinside [Swineside], Keswick, 35/2422, Jun 1879, *Wild* (BM). WALES: Pembrokeshire, v.-c. 45, Mynydd Carniningli, Prescelly Mts, 22/068373, *Janssens 915* (ALA*); Merioneth, v.-c. 48, (3; BBSUK, NY). SCOTLAND: Kirkudbrightshire, v.-c. 73, Kells Hills, 25/58, Sep 1961, *Peterken* (BBSUK); Wigtownshire, v.-c. 74, Main Water of Luce, 25/16, Apr 1955, *Lobley & Duncan* (BBSUK); Peebleshire, v.-c. 78, Ellers Cleuch, 36/1216, Jun 1968, *Milne-Redhead* (BBSUK*); West Perthshire, v.-c. 87, Ben Venue, 27/4706, Aug 1875, *Carrington* (DBN*); Mid Perthshire, v.-c. 88, Ben Challum, 27/3832, Jul 1866, *McKinlay* (BM); Easterness, v.-c. 96, Corrie an-t Sneachda, 28/9903, Jul 1909, *Wilson & Wheldon* (NMW); Westerness, v.-c. 97 (5; ALA, BM, E, NMW, UBC); Main Argyll, v.-c. 98 (6; ALA, BM, E, NMW, UBC); Dunbartonshire, v.-c. 99, Glen Loin, Arrochar, 27/30, Apr 1915, *Adam* (E); Clyde Isles, v.-c. 100, Arran, Gleann Easan Biorach, 16/946495, *Long 311* (E*); North Ebudes, v.-c. 104, Skye (2; ALA, E, NMW*); West Ross, v.-c. 105 (2, E); West Sutherland, v.-c. 108, S of Unapool, Assynt, 29/2429, *Schofield & Schuster 69976* (UBC); Outer Hebrides, v.-c. 110, Harris, Beinn na Teanga, 19/1602, Jul 1946, *Warburg* (BM*). IRELAND: West Cork, v.-c. H3, Coomataggart Mt., Sep 1953, *King* (DBN*); Mid-Cork, v.-c. H4, Musheragh Mt., May 1851, *Carroll* (BM); Down, v.-c. H38, Rocky Mountain near Hilltown, 33/2326, May 1923, *Lett* (DBN).

Differentiation and Relationships. *Andreaea megistospora*, as its name implies, is distinguished from all other *Andreaeae* by its very large spores, the largest in the genus. It is also recognizable by its relatively small size and its falcate leaves with the lamina distinct to the apex. In addition to spore size it is distinct microscopically from *A. rothii* ssp. *rothii* and *A. frigida*, the other species in the British Isles with similar leaves, by its papillose perichaetial bracts.

Subspecies *megistospora* and a second subspecies, ssp. *epapillosa* B. Murr. from British Columbia and Alaska, have been recently described and discussed (Chapter IV). *Andreaea megistospora* seems to be most closely related to *A. rothii*. Both species have large spores and occur at lower elevations than other members of sect. *Nerviae*. Perhaps this line diverged from a line defined by the presence of mid-sized spores and occurrence in wet, alpine habitats; see Table VI-3. If this is true, *A. megistospora* may be the most derived taxon in sect. *Nerviae*.

7. *Andreaea alpina* Hedw. (Fig. VI-8)

Sp. Musc. Frond. 49, pl. 7, fig. 2p. 1801. Types: "in alpibus Britanniae, rupibusque Sueciae, Bructeri, Germaniae," not seen.

A. alpina Hedw. var. *flavicans* Hook., *Trans. Linn. Soc. London* 10: 389. 1811. - Type: Scotland: Ben Nevis (?holotype, Scotland, *Hooker & Borrer*, BM-Hooker; isotypes, Ben Nevis, 1808, *Hooker & Borrer*, BM!, BM-Wilson!, BM-Wilson *ex* Hooker!, BM-Wilson *ex* Turner!, H-Lindberg!

A. alpina Hedw. var. *compacta* Hook., *Trans. Linn. Soc. London* 10: 389. 1811. - Type: Scotland: Ben Nevis, 1808, *Hooker & Borrer* (holotype: BM-Hooker; isotypes, BM-Wilson *ex* Hooker!, BM!

Nomenclature. I have not yet dealt with typification of *A. alpina*. I have not seen the type material. A note made in 1970 by E.

Nyholm, accompanying a slide in S, says that in G-Hedwig under *A. rupestris alpina* is *A. rupestris*, *Ehrhardt*, *A. obovata*, Suecia, O. Swartz herbarium and *A. alpina*, Ben Nevis, the latter considered the holotype by E. Nyholm.

In Hooker's herbarium at BM, there is a specimen labelled var. B Hooker, Scotland, without date, *Hooker & Borrer*, that is probably the holotype of var. *flavicans*.

Plants large to robust, reddish brown to purplish black. Protonemal appendages not seen. Stems 1-6(-8) cm high. Axillary hairs with brown, ± persistent, cylindric mucilaginous cells, stalk sometimes branched or multiseriate within perichaetium. Juvenile leaves denticulate and apiculate. Mature leaves when wet erect-spreading to squarrose; when dry little changed, erect to spreading, straight, stiff, to about 1.5 mm long, 0.7 mm wide, panduriform, broadest above constriction, symmetric, abruptly narrowed to incurved apices about 1/4-1/3(-1/2) the length of leaves, margins plane to incurved, denticulate from near bases into mid-leaf constriction due to projecting cell ends, appearing bordered by several rows of oblique, thinner walled cells that are also thinner in transverse section. Costa absent. Lamina mostly unistratose, occasionally locally bistratose or completely bistratose apically. Upper laminal cells round to oval, 8-10 μm wide, thick-walled, somewhat collenchymatous, papillae lacking. Transition from upper to basal cells ± abrupt. Basal cells rectangular to long-rectangular, lumens and walls ± equally thick, walls pitted and nodose, in transverse section dorsal walls bulging. Cladautoicous. Perigonial bracts occasionally papillose above, paraphyses numerous. Perichaetial bracts differentiated, large, sheathing and convolute, sometimes distant and slightly secund. Capsules common to occasional, medium-sized, about 1 mm long. Spore abortion frequent; spores medium-sized, shrivelled, brown spores 17-28 µm, turgid, green spores 26-38 µm, rarely larger.

Ecology. On wet to continuously dripping rocks in streams and on ledges and cliffs and on moist and periodically irrigated outcrops and boulders, from lowlands to highlands, 50 to 1300 m, apparently most frequent in mountains (Duncan 1966, Birks & Birks 1974, Smith 1978). (Størmer [1969], in contrast, reported that in Norway, although the altitudinal range was wide, most collections were made between sea level and a few hundred meters.) The substrate is acidic or, often, mildly basic rocks (granite, basalt, siliceous and calcareous schist, mica-schist); one collection from Shetland grew on "wet ground." Occasionally associated with other Andreaeae: A. rupestris, A. rothii ssp. falcata, A. megistospora ssp. megistospora, and A. mutabilis.

Andreaea alpina is one of the Andreaea species whose temperature response was studied by Dilks & Proctor (1975). It was found to have a broad optimum range of temperature for net assimilation, similar to those in A. rothii and Racomitrium lanuginosum, and also appeared to survive the lowest temperatures used in the experiment.

Distribution. Occasional to frequent in Wales, northern England, Scotland and Ireland. Of the 45 vice-counties reported for A. alpina by Corley & Hill (1981), I have not seen material from the following six: Pembrokeshire, v.-c. 45, South Northumberland, v.-c. 67, Selkirkshire, v.-c. 79, Sligo, v.-c. H28, Armagh, v.-c. H37, and Londonderry, v.-c. H40. To their list I can add Wigtownshire, v-c. 74.

Although widely distributed in the British Isles, A. alpina is most abundant in Scotland. Approximately 58 per cent of the material examined is from Scotland, 20 per cent from Wales, 12 per cent from northern England, and 10 per cent from Ireland. These figures no doubt reflect the greater amount of wet mountain habitat in Scotland. Størmer (1969) felt that in Norway distribution of A. alpina was primarily governed by precipitation, the species requiring high precipitation and atmospheric moisture such as occurs in highlands in the British Isles.

Known elsewhere in the North Atlantic region from the Faroes and Norway and recently reported from southernmost Greenland (Chapter V). Andreaea alpina is a bipolar species. In the Southern Hemisphere it is widely distributed on subantarctic and cold temperate islands: the Auckland Islands, Tasmania, Kerguelen Island, Marion Island, Gough Island, South Georgia, and the Falkland Islands, and along the west coast of South America as far north as Colombia. In this region it is part of a group of closely related taxa. In the Northern Hemisphere, however, it is taxonomically uniform and has no close relatives. Since A. alpina and its allies diversified and are widespread in the Southern Hemisphere, it is possible they originated there and were, therefore, secondarily distributed in the Northern Hemisphere. This is opposite to the trend postulated for bipolar bryophytes by Schuster for example (1983, p. 594) "Bipolar hepatics and mosses share one common feature: virtually all of them are clearly of holarctic origin: thus dispersal has been one way." Andreaea mutabilis is another bipolar species that occurs in Britain and is widespread in the Southern Hemisphere and may have originated there.

Specimens studied (Ca. 700; from v.-c. 42, 44, 46, 48, 49, 64-66, 68-70. 72-75, 78, 86-92, 94, 96-101, 103-108, 110, 112, H1, H2, H7, H16, H27, H35, H38, H39; in ALA, ALTA, B, BBSUK, BM, DBN, DUKE, E, H, MO, NMW, NY, S, UBC, Herb. Perry). New vice-county record: Wigtownshire, v.-c. 74, Main Water of Luce, above New Luce, grid reference 25/16, Apr 1955, Lobley & U. Duncan (BBSUK).

Differentiation and Relationships. Easily identified by its large size, rather coarse appearance, and its ecostate, symmetric, panduriform leaves that are denticulate along the lower margin and are abruptly contracted to the acute apex. The species varies from robust to small, with leaves crowded to distant, stiff to lax, and short- to long-tipped. The varieties of Hooker reflect some of these variations, which have no taxonomic significance.

Andreaea alpina has no close relatives in the Northern Hemisphere, but it is part of an interesting complex in the Southern Hemisphere that needs more study.

8. *Andreaea sinuosa* B. Murr. (Fig. VI-9)

Bryologist 89: 189, fig. 1-17. 1987. Type: Canada: British Columbia, West Vancouver, Schofield 74208 (holotype: UBC; isotype: ALA).

Plants small, green-brown, red-brown, purple-black or black. Protonemal appendages rarely seen. Stems rarely over 1 cm high, cells frequently sinuose in surface view. Axillary hairs with brown, persistent, cylindric or clavate mucilaginous cells. Juvenile leaves apiculate, occasionally sparsely toothed from projecting cells. Mature leaves sometimes appearing tristichous, when wet slightly spreading, when dry erect, more or less appressed, sometimes secund; to 1.6 mm long, to 0.35 mm wide, narrowly lanceolate to linear-lanceolate, broadest just above the only slightly sheathing base; apices acute or occasionally rounded; margins incurved, entire. Costa absent. Lamina unistratose or locally bistratose. Upper leaf cells irregularly rounded, oval or oblate, 10-12 μm, with large, low, brown to white papillae that are more numerous centrally than marginally or apically; ± thick-walled and collenchymatous. Laminal cells gradually larger and conspicuously pitted to sinuose towards the sheathing base, with papillae becoming sparse. Basal cells rectangular to oblong, lumens often scalariform, longitudinal walls incrassate, pitted and strongly sinuose as in Racomitrium, transverse walls thin; papillae absent, joint thickenings frequently visible in transverse section. Sexual condition undetermined, apparently dioicous, but stems very short and fragile, so possibly cladautoicous. Perigonial paraphyses few or lacking. Perichaetial bracts differentiated, convolute and sheathing. Capsules common, barely emergent to shortly exserted, small, about 0.8 mm long, capsule base usually occupying 1/2 or more of the capsule length. Spore abortion rare, spores small, (11)13-19(21) μm.

Ecology. On acidic rock in extreme snow-beds (Murray 1987). See also discussion of A. blyttii.

Distribution. Very rare. On high ground in Scotland where snow can persist, *ca*. 990-1100 m elevation. Otherwise known only from the Aleutian Islands, Alaska and British Columbia (Murray 1987).

Specimens studied (9). SCOTLAND: South Aberdeen, v.-c. 92: Beinn a'Bhuird, below S Top, grid reference 37/095977, 13 Jul 1985, *Murray & Long*, (ALA), *Long & Murray 12791* p.p. (E); Westerness, v.-c. 97: Ben Alder Forest, Geal-charn, 27/477748, 9 Jul 1981, *Gilbert, Fox & Purvis*, (BM Lichen Herbarium, under *Lecanora leptacina* Sommerf.); West Ross, v.-c. 105: Beinn Dearg, 28/259815, *Long 13791* (ALA, E); East Ross, v.-c. 106: Beinn Dearg, 18 km SE of Ullapool, grid reference 28/2681, *Coppins et al. ex Coppins 10534* (E).

Differentiation and Relationships. *Andreaea sinuosa* can be distinguished from all other ecostate *Andreaeae* by its strongly sinuose basal cell walls. It also has small spores, less than 21 um, unlike all *Andreaeae* in the British Isles except the costate *A. blyttii* and the ecostate *A. mutabilis*. In the field it can be confused with forms of *A. rupestris* var. *rupestris* with acuminate leaves that also occur on high mountains. *Andreaea sinuosa*, however, has less sheathing leaves with more strongly incurved margins.

The relationships of *Andreaea sinuosa* do not appear to be with the *A. rupestris* group; perhaps it has its closest relatives among costate taxa in sect. *Nerviae*, members of which also have sinuose cell walls, axillary hairs with persistent mucilaginous cells and infrequent spore abortion (Murray 1987).

9. *Andreaea mutabilis* Hook. f. & Wils. (Fig. VI-10)
Lond. J. Bot. 3: 536. 1844. *A. mutabilis* var. *microphylla* Hook. f. & Wils., *Lond. J. Bot.* 3: 536. 1844. Types: Auckland Islands, *J. D. Hooker 50* (lectotype, chosen by Vitt 1980: BM-Wilson!; isolectotypes: BM-Hooker!, BM!, FH!, ALTA!). Campbell Island, *J. D. Hooker 1b* (syntypes: BM-Wilson!, BM-Hooker!, FH!, ALTA!).

A. petrophila Ehrh. ssp. *tenella* Kindb., *Eur. N. Amer. Bryin.* 2: 393. 1897, *syn. nov.* Type: Spain, Pyrenees, hospice de Vénasque, August 1855, *Kindberg* (holotype: S-Kindberg!; isotypes: BM!, S!).

A. hohuanensis Chuang, *J. Hattori bot. Lab.* 37: 427, fig. 3. 1973, *syn. nov.* Type: Taiwan: Nantou region, Mt. Ho-huan-shan, *Chuang 5914* (holotype: UBC!).

Plants small, rarely medium-sized, purple-red to black, sometimes glaucous (from dense papillae) or green-black. Protonemal appendages not seen. Stems rarely over 1 cm high. Axillary hairs often with persistent, brown mucilaginous cells. Juvenile leaves lanceolate. Mature leaves when wet spreading, when dry erect-spreading, not clasping, sometimes secund, often distant, usually less than 1 mm long, to about 0.35 mm wide, lanceolate, usually symmetric, apices acute, margins often incurved, entire. Costa absent. Lamina mostly unistratose, occasionally locally bistratose above. Upper laminal cells round to oval, 9-12 µm, thick-walled, ± pitted, papillose. Transition from upper to basal cells gradual, cells papillose to near base. Basal cells at margin isodiametric to oblate, central cells elongate, thick-walled, little pitted, an irregularly shaped yellow patch often seen in leaf bases. Cladautoicous. Perigonia numerous, crimson, paraphyses not seen. Perichaetial bracts differentiated, sheathing and convolute. Capsules common, small, less than 1 mm long. Spore abortion occasional, spores 12-21(very rarely to 32) um.

Ecology. On dry to wet acidic rocks (granite, andesite, basalt, quartzite), occasionally on humus over rock. *A. mutabilis* occurs most frequently on mountains between 600-1225 m (several collections between 150-250 m). Occasionally closely associated with other *Andreaeae*, especially *A. rupestris* and *A. alpina*.

Distribution. New to the Northern Hemisphere, including the British Isles, where it is occasional in Scotland and rare in northern England and North Wales. Of the 80 odd collections seen from Britain about 77 per cent are from Scotland, 16 per cent from northern England and 6 per cent from North Wales. I have also seen other European material from France and Spain, and one collection from Canada (British Columbia).

Andreaea mutabilis is widespread in the Southern Hemisphere. Details of its taxonomy and interesting bipolar distribution will be presented elsewhere. In brief, in addition to Europe and North America, I have seen specimens of *A. mutabilis* from: Ecuador, Argentina, Falkland Islands, Tristan da Cunha, Kerguelen Island, Australia, Tasmania, New Zealand, Macquarie Island, Auckland Islands, Campbell Island, New Guinea, Celebes, Borneo, and Taiwan.

Specimens studied (Ca. 80). ENGLAND: West Lancashire, v.-c. 60, Greenbank Fell, grid reference 34/66, Oct 1899, Wilson & Wheldon (NMW); North-west Yorkshire, v.-c. 65, Cantley Crags, 34/6896, May 1905, West (BM); North Northumberland, v.-c. 68, 36/82, Sep 1930, J. B. Duncan & Lobley (BBSUK); Westmorland, v.-c. 69, Helvellyn (4; BBSUK, BM, DBN, E); Cumberland, v.-c. 70 (5; BM, E, NMW). WALES: Caernarvonshire, v.-c. 49, Snowden vicinity (5; BM, E, NMW). SCOTLAND: Kirkudbrightshire, v.-c. 73, Moorbrook Hill, 25/6198, Oct 1951, Milne-Redhead (NMW); Lanarkshire, v.-c. 77, Tinto Hill, 26/9534, Jun 1935, Mackechnie (herb. Wallace); Fife, v.-c. 85, Glen Queich, 37/00, Apr 1904, Evans (E); West Perthshire, v.-c. 87, Uamh Mhor, 27/6811, Aug 1866, McKinlay (BM, H); Mid Perthshire, v.-c. 88, Ben More, 27/42, Jul 1875, George (BM, H); Angus, v.-c. 90, Caenlochan Glen, 37/1777, Jul 1985, Murray & Long (ALA, E); South Aberdeenshire, v.-c. 92 (6; ALA, BM, E, herb. Wallace); Banffshire, v.-c. 94, 27/9999, Ben MacDhui, Jul 1909, Wilson & Wheldon (BM, DBN, E, NMW); Easterness, v.-c. 96 (11; ALA, BBSUK, BM, E, NMW, herb. Wallace); Westerness, v.-c. 97, (20; ALA, BBSUK, BM, E, NMW, UBC, herb. Wallace); Main Argyll, v.-c. 98 (9; ALA, BBSUK, BM, E, NMW); Mid Ebudes, v.-c. 103, Mull, Ben More, 17/5133, Aug 1966, Corley (BM); West Ross, v.-c. 105, Beinn Dearg, 28/259815, Long 13789 (E).

Differentiation and Relationships. Andreaea mutabilis is easily recognized by its basal cells that are marginally isodiametric and centrally little pitted. There is often a striking yellow patch at the base of leaves. It also has small spores and leaves that are not at all, or only very slightly, sheathing, both unusual features in Andreaeae. Leaves tend to be more distant in A. mutabilis than in other ecostate species, with the result that the non-clasping leaf bases and insertions are often clearly visible. In the field *A. mutabilis* is likely to be mistaken for *A. rupestris* or *A. alpestris*, but it tends to occur in small, flattened, spreading cushions and to be purple-red (rarely glaucous from dense papillae) in color. It is often recognizable by the small flattened cushions with numerous tiny crimson male plants. *Andreaea mutabilis* has been considered a dioicous species, but I have seen cladautoicous material from several British localities and from Tristan da Cunha.

It is interesting that although *A. mutabilis* was described (from Australasia) by the British botanists J. D. Hooker and W. Wilson (Hooker 1844), they did not recognize it in Britain. Although he did not notice the diagnostic isodiametric basal marginal cells, Wilson did mention the non-clasping leaf bases (key in Hooker 1844), and Wilson and Hooker did describe the conspicuous yellow bases (Hooker 1845). McKinlay's collection of *A. mutabilis* from Uamh Mhor (reported by Braithwaite [1880-1887] as *A. petrophila* var. *alpestris*) is present in Wilson's herbarium in BM with drawings and a note suggesting it be compared with *A. sparsifolia* Zett. and that according to Schimper it is "alpestris var." There is also another note on the herbarium sheet "....I also enclose a scrap of *A. alpestris* from Uam Mhor authenticated by Schimper as a 'var. ad *A. petrophila* var. *gracilis* vergens'....McKinlay in lit. 7 Aug 1866."

Many specimens cited by Braithwaite (1880-1887) as various varieties of *A. petrophila* (= *A. rupestris*) are in fact *A. mutabilis*--especially vars. *flaccida* Schimp., *gracilis* Schimp., and *sparsifolia* (Zett.) Lindb. The only report of var. *sparsifolia* from Britain

(Braithwaite 1880-1887 as a variety of *A. petrophila*, Smith 1978 as a variety of *A. obovata*) is referable to *A. mutabilis*.

Another eminent British bryologist with Southern Hemisphere experience with *A. mutabilis* was H. N. Dixon. Dixon (1929) tried to sort out the 30 or so *Andreaea* species that had been recorded from New Zealand. After much hesitation he synonymized *A. mutabilis* and *A. rupestris* (as *A. petrophila*). It is clear from his writings and annotations that he did not understand *A. mutabilis*, since the only character he considered important for it was the occasionally crenate leaf margin which he said he observed in some of Hooker's original material. Leaf margins of *A. mutabilis* are entire; my study of specimens annotated by Dixon shows that he confused several taxa in the *A. acutifolia* group with *A. mutabilis*, most often *A. acuminata* Mitt. Later Dixon (Dixon & Bartram 1937) recognized a plant, to which he gave the name *A. schimperi* Dix., as a species distinct from *A. rupestris* on account of, among other things, its isodiametric basal marginal cells, but he did not recognize it as the same as *A. mutabilis* (Vitt 1980). As had Schimper, Dixon, when studying material from Britain referable to *A. mutabilis*, tended to call it *A. alpestris* (as *A. petrophila* var. *alpestris*). A specimen in BM (Cairngorm, July 1930, *Knight*, *Jones & Duncan*) was identified as var. *gracilis*, which was crossed out by Dixon and replaced with var. *alpestris*. There is in addition a note by Dixon: "I do not think this is the var. gracilis, which has rather long distant leaves. It may, I think very well be var. alpestris Thed. which continental botanists seem to find as distinct but I cannot find it is!"

The systematic relationships of A. mutabilis are unclear. It does not seem to have close relatives among other ecostate species with isodiametric basal marginal cells (distributed in the Southern Hemisphere), except perhaps A. leiophylla Card. ex Roth.

10. Andreaea rupestris Hedw., Sp. Musc. Frond. 47., pl. 7, fig. 2g-o. 1801. Types: Europe (ALTA ex G-Hedwig!).

A. petrophila Ehrh. ex Fürnr., Flora 10(Beibl. 2): 30. 1827.

Plants medium-sized to large, green-bronze, red-brown to black. Stems rarely more than 3 cm high. Protonemal appendages seen. Juvenile leaves ovate to lanceolate, acute. Mature leaves variable, when wet widely spreading to squarrose, when dry appressed, spreading, squarrose, or sometimes imbricate; straight to secund, ovate- to oblong-lanceolate, little constricted above bases or panduriform, broadest above or below constriction, usually less than 1 mm long and 0.5 mm wide, apices usually oblique, often secund, often incurved, obtuse or acute, short or sometime long, gradually formed, margins plane or ± incurved. Costa absent. Lamina unistratose, upper cells quadrate to short-rectangular, lumens variable, rounded, oval to irregular, stellate or short-rectangular, about 8-10 µm wide, walls usually thick, 2-6 µm, usually strongly pitted, collenchymatous, characteristically with prominent, whitish cuticular dorsal papillae that are longer than wide, sometimes epapillose. Transition from upper to basal cells ± abrupt. Basal leaf cells variable, short- to long-rectangular, lumens wider or much narrower than walls, bulging or not, walls pitted, sometimes strongly so and nodose. Basal marginal cells quadrate, oblate or short-rectangular. Cladautoicous. Perigonia small, paraphyses few. Perichaetial leaves differentiated, sheathing and convolute, usually strongly papillose. Capsules common, medium sized, about 1 mm long. Spore abortion frequent, shrivelled brown spores usually 20-24 µm, turgid green spores 26-32(-48, rarely larger) µm.

10a. Andreaea rupestris var. rupestris (Fig. VI-11a-h,i[upper],j,k,m-p)

Nomenclature. The following varieties of A. rupestris (as A. petrophila) described by Schimper (Bruch, Schimper & Gümbel 1855) have been reported from the British Isles (e.g. Braithwaite 1880-1887), vars. acuminata, flaccida, sylvicola, and gracilis. I have examined material of A. rupestris in Schimper's herbarium at BM, and I have not been able to typify these names, nor do most illustrations in Bruch, Schimper & Gümbel (1855) appear distinct from forms that I consider var. rupestris. As discussed in Chapter V, Schimper, himself, attached little importance to the forms represented by the names. He stated that he simply wanted to describe the diversity he saw within the polymorphic species, A. rupestris, and to prevent unnecessary naming of new species. Sharp (1936), without examining types, treated A. papillosa Lindb. and var. acuminata as synonyms, but I do not think that there is evidence to support this decision.

Plants rupestral, very rarely on lithosols. Stems rarely more than 3 cm high. Leaf apices short or long, gradually formed. Papillae (when present) longer than wide but rarely twice as long as wide.

Ecology. Most commonly forming greenish or black cushions on neutral to acidic boulders, cliffs or walls (basalt, mica-schist, sandstone, granite) that are dry or seasonally wet; also in snow-beds. Very rare on lithosols. Found in lowlands and mountains (from near sea level to about 1225 m). Often in drier sites than most other Andreaea species. Apparently widely tolerant of various ecological factors (aspect, elevation, substrate, moisture); usually associated with other Andreaeae, including most species found in the British Isles. The only Andreaea habitats that seem unsuitable for var. rupestris are continuously wet sites such as streams and flushes.

Distribution. Common in suitable habitats throughout the British Isles. However, much more frequent in Scotland than elsewhere. Almost 60 per cent of the material seen came from Scotland and about 10 per cent from Ireland, 12 per cent from Wales, and 18 per cent from England. I have seen material from about 72 vice-counties from southwestern England to the Shetlands and throughout Ireland. Reported from 85 vice-counties by Smith (1978) and from 92 by Corley & Hill (1981). I have not seen material from the following vice-counties reported by Corley & Hill (1981) in the herbaria whose specimens I have studied: v.-c. 14, 43, 47, 63, 71, 74, 76, 77, 100-103, 107, H1, H2, H7, H11, H12, H27. The following vice-counties apparently have new records of var. rupestris: H4 and H34 (cited below).

Of approximately 570 specimens of var. rupestris studied, about 35, or 6 per cent, had features intermediate to those of var. papillosa. These specimens in which only some leaves had abruptly formed, long apices occur throughout the range of var. rupestris and appear to be of no taxonomic significance. An asterisk (*) following a vice-county in the list of specimens studied, indicates that intermediate material was seen as well as typical var. rupestris.

A widespread taxon, known elsewhere from Europe, the Caucasus, Asia, Japan, Pacific Islands, and North America. Reported from Central and South America, Antarctica, southern Africa, Tasmania and New Zealand.

Specimens studied (Ca. 570; from v.-c. 1,3*, 4, 40, 41, 42*, 44*, 45*, 46, 48*, 49*, 50, 59, 60, 62, 64*, 65*, 66-68, 69*, 70, 72, 73, 75, 78-80, 81*, 82-91, 92*, 93, 94*, 95, 96*, 97*, 98, 99, 104-106, 108-112, H3, H4, H6, H8, H13, H16, H20*, H21, H29-H31*, H34-H37, H38*, H39*, H40). IRELAND: Mid-Cork, v.-c. H4, Musheragh Mt., grid reference 10/3285, May 1851, Carroll (BM); East Donegal, v.-c. H34, Inishowen Mt., 24/34, no date, R. Brown (BM).

Differentiation and Relationships. Andreaea rupestris is a polymorphic species, as is its var. rupestris. Variety rupestris can usually be distinguished from other ecostate species by the combination of asymmetric, secund, papillose leaves with rectangular basal marginal cells, pitted to nodose (but not sinuose), thick-walled basal cental cells, collenchymatous upper cells, and by its medium-sized spores. Andreaea rupestris is closely related to A. alpestris (it is not without hesitation that I treat them as separate species). Experimental growth studies are required to assess or try to solve the taxonomic problems of *A. rupestris* and its allies. Small forms of var. *rupestris* with less secund leaves, few or no apparent papillae, and less pitted and collenchymatous cells than typical are very difficult if not impossible to place. If leaf apices tend to be secund, laminae unistratose, and at least some cells are pitted, collenchymatous and papillose, I treat the material as var. *rupestris*. Variety *papillosa* shares the same variability but has leaves with long and abruptly formed apices. Leaves of var. *rupestris* (and var. *papillosa*) are often panduriform and symmetric, but they are usually strongly papillose and the tip is usually oblique, which distinguishes them from *A. obovata* (= *A. hartmannii*), another closely related species, which is of doubtful occurrence in the British Isles and is not treated here.

Although the most common form of var. *rupestris* has leaves with short, obtuse, secund apices (Fig. VI-11n,o), there is another occasional form in mountains with acuminate leaves (Fig. VI-11m). This form has usually been called var. *acuminata* Schimp. In Britain this material, has sometimes been treated as var. *papillosa*, but I (arbitrarily) treat it as var. *rupestris*, since the acumen is gradually rather than abruptly formed.

10b. *Andreaea rupestris* var. *papillosa* (Lindb.) Podp. (Fig. VI-11,i [lower],l).

Consp. Musc. Eur. 45. 1954. *A. papillosa* Lindb., *Ofv. K. Vet. Ak. Förh.* 23: 557 1867. *A. obovata* Thed. var. *papillosa* (Lindb.) Nyh., *Illus*. *Moss Fl*. *Fennoscand*. 2(fasc 6): 691. 1969. Types: Spitzbergen (syntypes: H!).

A. *sparsifolia* Zett., *Monogr*. *Andreaearum* *Scand*. 32. 1855. *A*. *obovata* Thed. var. *sparsifolia* (Zett.) Nyh., *Illus*. *Moss* *Fl*. *Fennoscand*. 2(fasc. 6): 691. 1969. Type: Norway (UPS!, BM!, S!).

Plants small, or (on soil) commonly large and robust. Stems often over 3 cm high. In robust material (extra-territorial) leaves to about 2 mm long and 0.6 mm wide, apices acute, often very long and abruptly formed from ovate bases. Prominent whitish cuticular papillae often over twice as long as wide, rarely low and inconspicuous.

Ecology. Little information from Britain is available. On acidic rocks in mountains. In the Arctic var. *papillosa* often grows on lithosols.

Distribution. Very rare. The few collections that I have identified as var. *papillosa* do not represent typical robust material. Primarily an Arctic taxon, found to the south only in mountains of northern Europe, Asia, and North America. British material is from the southern edge of its range and is depauperate (even equivocal). Reported (as *A*. *obovata* var. *papillosa*) from 17 vice-counties by Smith (1978) and from five by Corley and Hill (1981). Most of their records probably fit my concept of acuminate var. *rupestris* (Fig. VI-11m).

Specimens studied (4). ENGLAND: Cumberland, v.-c. 70, Swinside [Swineside], Keswick, grid reference 35/2422, Jun 1879, *Wild* (BM). WALES: Merioneth, v.-c. 48, near Dolgellau, Jul 1964, *Townsend* (herb. Townsend); Caernarvonshire, v.-c. 49, Carnedd Llewelyn, Sep 1978, *Townsend* (herb. Townsend). IRELAND: South Kerry, v.-c. H1, Mt. Eagle, 00/3398, Apr 1857, no collector (BM-Wilson).

Differentiation. Distinguished from var. *rupestris* by the much longer and more abruptly formed leaf apices (Fig VI-11l) and by its frequent occurrence on soil (outside Britain) as well as rock. Small rock forms with gradually formed very long apices are difficult to treat, and taxonomic decisions are arbitrary. Most long-tipped material from Britain has gradually formed apices (Fig. VI-11m), and I have referred this material to the var. *rupestris*. Fig. 29: 5 & 6 of *A. obovata* var. *papillosa* (in Smith 1978) appear to me to represent long-tipped var. *rupestris* rather than var. *papillosa*. Although var. *papillosa* is very distinct in the Arctic, to the south it is difficult to separate from var. *rupestris*, and the variation may prove to be clinal (see Chapter V). Sharp (1936) considered *A. rupestris* var. *acuminata* Schimp. a synonym of *A. papillosa*. I agree with Mårtensson (1956) that in the absence of type material for var. *acuminata* and with a plate (Bruch, Schimper, & Gümbel 1855, pl. 2(624) that shows leaves intermediate between the two varieties as well as typical of var. *papillosa*, it is preferable to accept Lindberg's name. The polymorphic nature of *A. rupestris* is further pointed up by the treatment of var. *papillosa* as an infraspecific taxon of either *A. rupestris* (Jensen 1939, Sharp 1936, Mårtensson 1956, and myself) or *A. obovata* (Nyholm

1969). Nyholm's position is one to which I have little trouble subscribing, having seen material of var. papillosa with panduriform leaves and apices of various lengths that is very close to A. obovata. (Schimper's A petrophila var. robusta is probably this plant [Bruch, Schimper, & Gümbel 1855].) The situation clearly cannot be sorted out without experimental work. Meanwhile, I feel that arctic material of var. papillosa is so distinctive that it should be recognized taxonomically. And since panduriform leaves are not uncommon in var. rupestris and well-developed white papillae are not characteristic of A. obovata, I am treating var. papillosa as closer to var. rupestris than to A. obovata.

The reports of A.obovata var. sparsifolia (Braithwaite 1880-1887 as A. petrophila var. sparsifolia [Zett.] Lindb., Smith 1978) from Britain are based on a misidentification. The collection (Ben More, George [BM, H]) is A. mutabilis.

11. Andreaea alpestris (Thed.) Schimp. (Fig. VI-12)
In Bruch, Schimper & Gümbel, Bryol. Eur. 6: 146, pl. 4(626). 1855.
A. petrophila Fürnr. var. alpestris Thed., Bot. Not. 5: 79, fig. 45-47. 1849. A. rupestris Hedw. var. alpestris (Thed.) Sharp., in Grout, Moss Fl. N. Amer. 1: 2. 1936. Type: Sweden, Herjedalen, Aug 1842, Thedenius (ALTA!, S!, UPS!)

Plants medium-sized (in Britain) to large, characteristically brown, brown-black to black, occasionally reddish. Stems 1-4 cm high. Leaves quite uniform, when wet widely spreading from waists, when dry imbricate and appressed, very rarely secund distally, stiff or soft, lanceolate, usually little constricted above bases, rarely panduriform, 0.5-1.0 mm long, rarely longer, 0.25-0.4 mm wide, apices straight or occasionally oblique, short, incurved, obtuse, rarely acute, margins plane or slightly incurved. Costa absent. Upper lamina unistratose or often with irregular, central bistratose patches, cells regular, ± quadrate, lumens rounded to oval, (7)8-10(11) μm wide, walls usually thin, 2-3(rarely to 6) um, not pitted, weakly collenchymatous, papillae present but low, inconspicuous, irregular, not white, dorsal, ventral also only in bistratose patches. Cells become very gradually longer toward leaf bases. Basal cells short-rectangular, lumens often bulging, up to twice as wide as walls, walls weakly pitted. Basal marginal cells oblate, rounded or short-rectangular. Reportedly autoicous. Perigonia small, paraphyses few. Perichaetial leaves differentiated, sheathing, convolute, with low, very rarely whitish papillae. Capsules infrequent, small to medium-sized, usually less than 1 mm long. Spore abortion frequent, shrivelled brown spores 16-21 μm, turgid green spores (21)22-26(32) μm, very rarely over 30 μm.

Ecology. In wet to dry, or seasonally wet habitats; forming small cushions on rock or large mats on lithosols in alpine areas (1070-1250 m) of Scotland and Wales (one scanty collection).

Distribution. Very rare in Scotland. I have seen one depauperate, doubtful collection from Wales. Reported from 12 vice-counties by Smith (1978) and from 13 by Corley & Hill (1981). I have re-identified material cited from Cumberland, v.-c. 70 (Borrowdale, Aug 1889, Dixon, BM) as A. rupestris var. rupestris. I have not seen material from vice-counties 86-88, 98, and 110, and I can add a record for vice-county 106.

Primarily a northern species, known from Europe, U.S.S.R., North America, and Greenland. Other reports are doubtful, since most southern material reported is misidentified.

Specimens studied (21). WALES: Caernarvonshire, v.-c. 49; Snowdon, grid reference 23/6054, Aug 1879, Cash (E) [scanty material]. SCOTLAND: Angus, v.-c. 90 (4: ALA, BM, H); South Aberdeenshire, v.-c. 92 (6; ALA, BM, DBN, E); Banffshire, v.-c. 94 (2; BM, herb. Wallace); Easterness, v.-c. 96 (2; ALA, E); Westerness, v.-c. 97 (5; ALA, DUKE, E, UBC, herb. Wallace); North Ebudes, v.-c. 104, Rhum, Ruinsival, 17/3594, Jun 1941, Heslop Harrison (herb. Wallace); East Ross, v.-c. 106, Beinn Dearg, 28/261814, Long 13807 (E);

Differentiation and Relationships. A. alpestris is morphologically uniform. Important features are the slender stems that appear thread-like and are usually a soft brown-black shade, occasionally a glossy black. The apices of the imbricate leaves are usually obtuse, straight and incurved; and papillae, though present, are low--not white or conspicuous. Microscopically, it is characterized by thin-walled, mostly unpitted cells with rounded lumens, and in many specimens bistratose patches occur in occasional leaves in the upper lamina. The transition in cell length from leaf base to apex is very gradual. Frequently described as much smaller than other Andreaea species, and this is only relatively true. Robust material (outside Britain) is similar in size to most other species. Similarly, leaf cell size is variable. Small forms of *A. alpestris* on rock can be very difficult to distinguish from *A. rupestris*, and sometimes the distinction is arbitrary. *Andreaea alpestris* is very rare in Britain, and most collections are of small rock forms, which cause difficulty. Most material I have seen previously identified as *A. alpestris* from Britain is better referred to *A. rupestris* var. *rupestris* or *A. mutabilis*.

It is with great hesitation that I treat *A. alpestris* as a species rather than as a variety of *A. rupestris*. Until experimental propagation is done, any judgment is doubtful. For now, I choose to emphasize the weak morphological distinctions: bulging lumens, locally bistratose apices, epapillose leaves and somewhat smaller spores, along with the tendency to grow in sterile mats on lithosols, to differentiate *A. alpestris* from *A. rupestris*. These features are much more apparent in northern than in British material.

Doubtful Species

Andreaea obovata Thed. The report of this species (as *A. hartmannii* Thed.) from Rhum (Heslop Harrison & Cooke 1942) has been considered doubtful by British bryologists (Richards & Wallace 1950, Smith 1978, Corley & Hill 1981). See discussion under *A. blyttii*.

Acknowledgements

I am very grateful to David G. Long and A. Roy Perry for guidance and excellent company in the field, for localizing records, sending publications, and for hospitality and help during visits to E and NMW. I also want to thank David Long for suggesting detailed mapping and offering to help. Without his organizing and checking most of the 2400 records, and the aid of A. R. Perry and D. M. Synnott, it would not have been possible. I am also very grateful to Kay W. Holmes for her help, care, and skill in making the line drawings and preparing the figures. C. D. Preston and the staff of the Biological Records Centre, NERC, Huntingdon, kindly agreed to accept the deposit of records of specimens seen and to produce distribution maps. I am most grateful to them. Others have also helped in various ways to make this study so enjoyable: permitting me to accompany them in the field, lending specimens, sending publications, giving hospitality, and sharing information. I thank them all, including: H. M. Perry, B. J. Coppins, B. Coppins, O. L. Gilbert, B. W. Fox, M. E. Newton, A. Eddy, A. R. Harrington, L. T. Ellis, E. C. Wallace, C. C. Townsend, P. Isoviita, B. J. O'Shea, M. O. Hill, A. J. E. Smith, M. F. V. Corley, N. Hodgetts, M. E. Edwards, and P. W. James. I am grateful to curators and staff of the following herbaria for lending specimens or providing help and space during visits: ALTA, B, BBSUK, BM, C, DBN, DUKE, E, FH, H, K, MO, NMW, NY, S, UBC. The University of Alaska Museum supported field work.

Table VI-1. Numbers and distribution of *Andreaea* species within the British Isles

	Number of species			
	Total	Alpine	Lowland	Indifferent
British Isles	11	6	2	3
Scotland	11	6	2	3
England	6	1	2	3
Wales	7	2	2	3
Ireland	4	0	2	2

Table VI-2. Infrageneric classification of *Andreaea* in Britain and Ireland and numerical list of taxa

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Andreaea Hedw.

Subgenus *Chasmocalyx* (Braithw.) Lindb. *in* Limpr.

Section *Chasmocalyx*

1. *A. nivalis* Hook.

Subgenus *Andreaea*

Section *Nerviae* Card. *ex* Broth.

2. *A. blyttii* Schimp.
3. *A. crassinervia* Bruch
4. *A. frigida* Hüb.

5a. *A. rothii* Web. & Mohr ssp. *rothii*

5b. *A. rothii* ssp. *falcata* (Schimp.) Lindb.

6. *A. megistospora* B. Murr. ssp. *megistospora*

Section *Andreaea*

7. *A. alpina* Hedw.
8. *A. sinuosa* B. Murr.
9. *A. mutabilis* Hook. f. & Wils.

10a. *A. rupestris* Hedw. var. *rupestris*

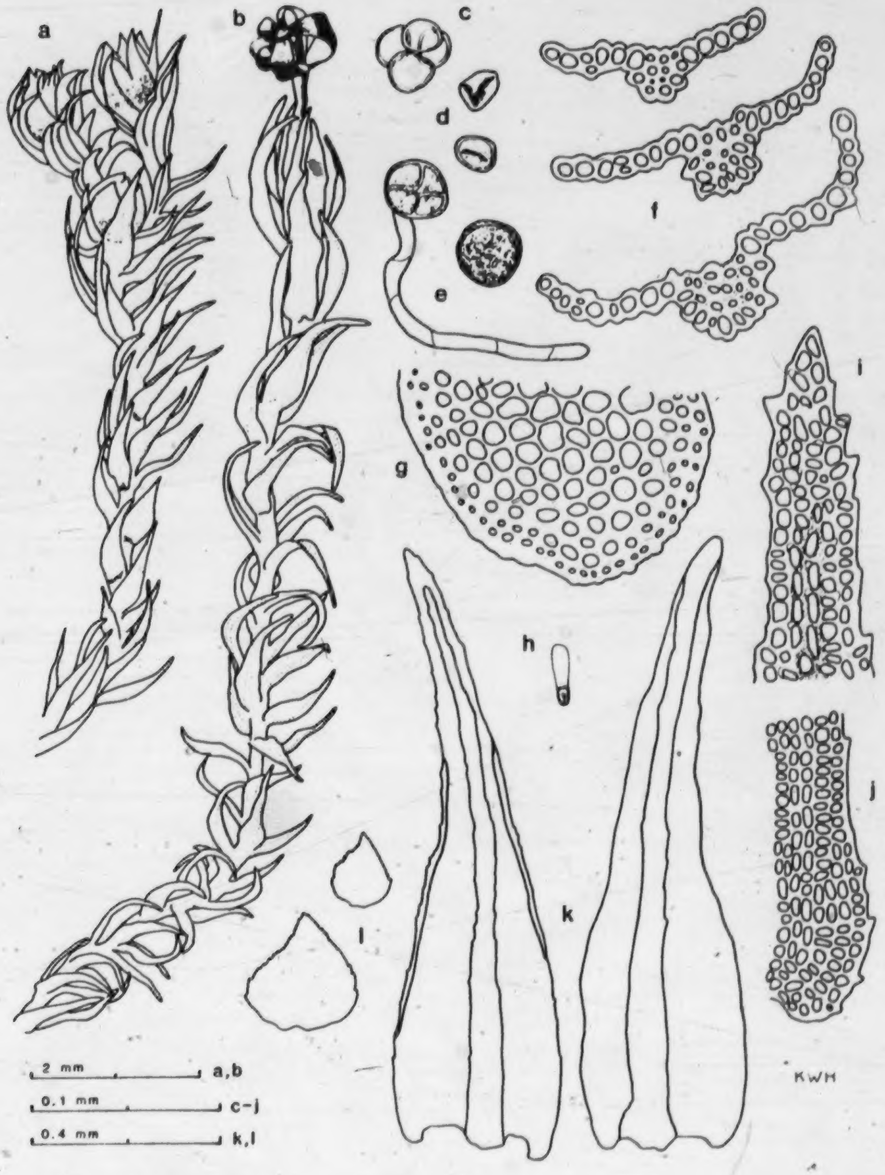
10b. *A. rupestris* var. *papillosa* (Lindb.) Podp.

11. *A. alpestris* (Thed.) Schimp.

Table VI-3. Comparison of *Andreaea* taxa in section *Nerviae* in the British Isles

	blyttii	*frigida*	*crassinervia*	*rothii*		*megistospora*
				ssp. *rothii*	ssp. *falcata*	ssp. *megistospora*
Spore size	small, (10)11-19(23) um	mid-sized, (20)25-35(40) um	mid-sized, (20)26-36 (40-50) um	large, (30)36-52(60-80) um		very large, (40)50-90 (110) um
Leaf taper	limb ± abruptly formed	lanceolate or limb gradually formed	limb ± abruptly formed	limb ± abruptly formed		limb ± abruptly formed
Lamina in upper part of leaf	indistinct	distinct	indistinct	distinct	indistinct to distinct	distinct
Costa	excurrent, almost completely filling subula	percurrent to excurrent and filling uppermost part of leaf	excurrent, almost completely filling subula	percurrent to excurrent and filling uppermost part of leaf	excurrent, usually filling upper subula, rarely percurrent	percurrent to excurrent and filling uppermost part of leaf
Transition between lamina and costa above shoulder	indistinct, costa not bulging dorsally	± distinct, costa biconvex or bulging dorsally	indistinct, costa not bulging dorsally	± distinct, costa bulging dorsally		distinct, costa biconvex to bulging dorsally
Basal marginal cells	mostly rectangular	mostly isodiametric	mostly isodiametric	mostly isodiametric	mostly isodiametric	mostly isodiametric
Sexuality	dioicous	autoicous	autoicous	autoicous	autoicous	autoicous
Perichaetial bract ornamentation	papillae absent to low and scattered	papillae absent	papillae present, usually scattered, or absent	papillae absent, rarely very low and scattered	papillae present, high and dense, rarely lacking in some plants within a population	papillae present, low to rarely high
Ecology	alpine (extreme snowbed); wet to seasonally dry	alpine; wet	alpine; wet	predominately lowland, reaching low alpine; dry to occasionally wet		predominately lowland, reaching low alpine; dry to occasionally wet
Distribution	circumalpine	Europe	Europe and eastern North America	Europe and North America (reported from Mongolia)	Europe and one collection seen from Oregon	northwestern Europe and northwestern North America

Figure VI-1. Illustrations of Andreaea nivalis: a, habit, male plant; b, habit, plant with sporophyte; c, tetrad; d, shrivelled spores; e, turgid and germinated spore; f, transverse sections of upper part of leaves; g, transverse section of stem; h, axillary hair; i, cells in upper part of leaf; j, marginal cells of leaf base; k, mature leaves; l, juvenile leaves. (a-e, f [two upper], g, k [right], l from Cairn Gorm, 2 Aug 1984, Murray & Perry, ALA; f [lower], i, k [left] from Ben Nevis, Long 13547, E; h, j from Aonach Beag, Long 13666, E)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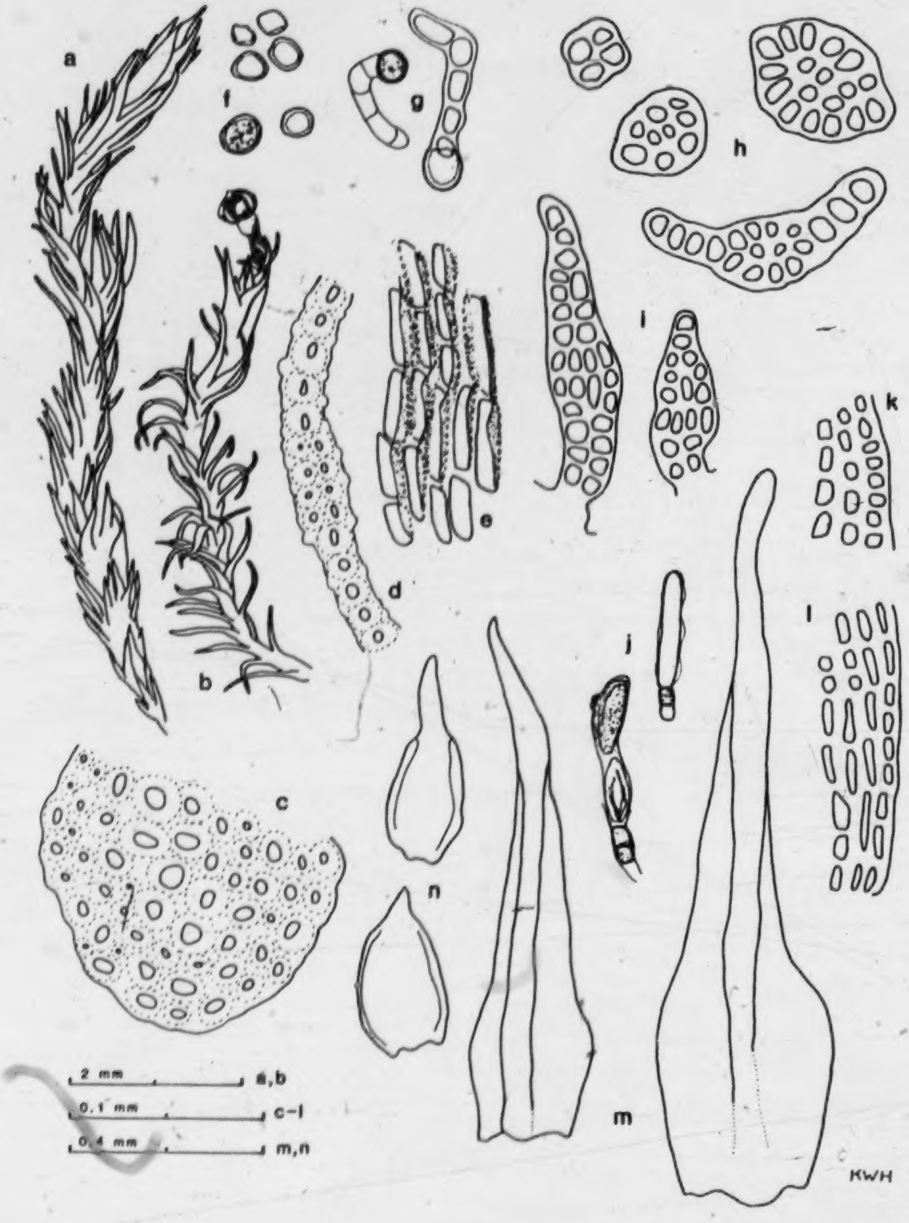
KWM

Figure VI-2. Illustrations of Andreaea blyttii: a, habit (dry), female plant with perichaetium; b, habit, plant with sporophyte; c, transverse section of stem; d, transverse section of perichaetial bract, showing joint thickenings; e, surface view of cells of perichaetial bract, showing joint thickenings f, spores; g, germinated spores; h, transverse sections of upper part of leaves; i, protonemal appendages; j, axillary hairs, lower from perichaetium; k, cells in upper part of leaf; l, marginal cells of leaf base; m, mature leaves; n, juvenile leaves. (a, f, h [upper right], i, j [upper], k-m from Beinn a'Bhuird, 13 Jul 1985, Murray & Long, ALA; b from Alaska, Murray 11343, ALA; c-e, g, h [three to left], j [lower], n from Beinn Dearg, Long 13798, ALA)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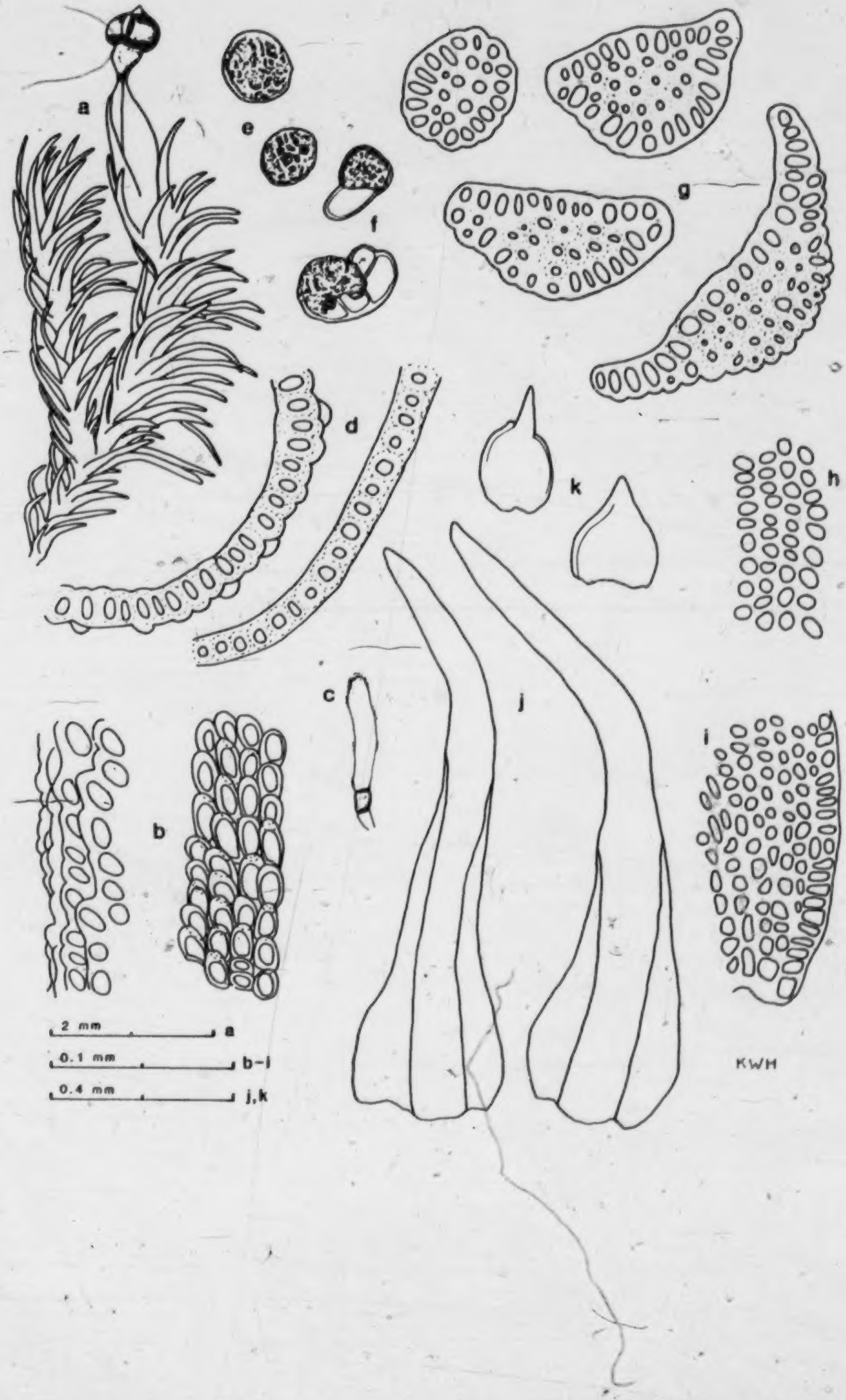
0.4 mm
m,n
KWH

Figure VI-3. Illustrations of Andreaea crassinervia: a, habit, plant with sporophyte; b, papillose cells of perichaetial bracts, side view and surface view, c, axillary hair; d, transverse sections of papillose and epapillose perichaetial bracts; e, spores; f, germinated spores; g, transverse sections of upper part of leaves; h, cells in upper part of leaf; i, marginal cells of leaf base; j, mature leaves; k, juvenile leaves. (a-d, g, k from type, Switzerland, Grimsel, Maerker, BM-Bruch in herb. Schimper; e, f, h-j, from Dhuloch, ?1870, Fergusson, NY)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a
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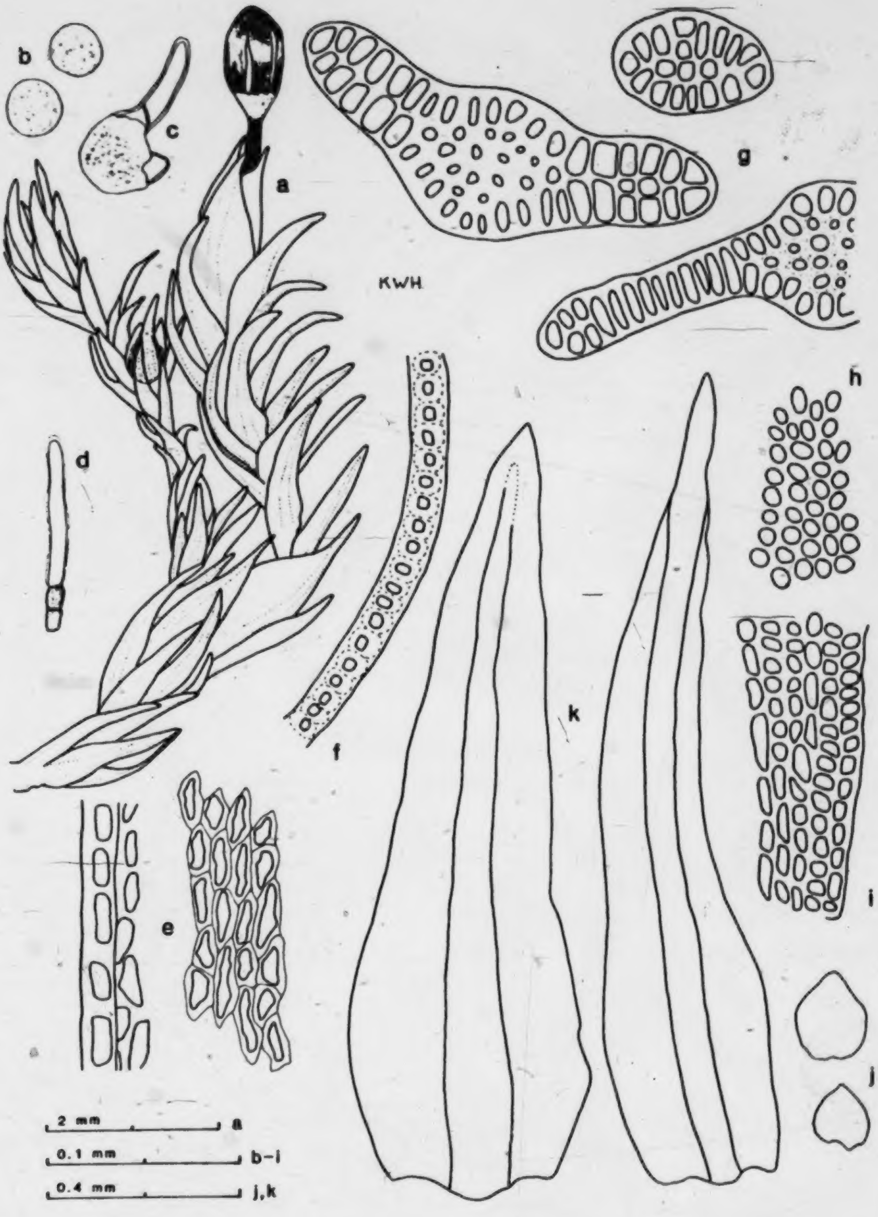
b–i
0.4 mm
j,k
KWH

Figure VI-4. Illustrations of _Andreaea frigida_: a, habit, cladautoicous plant with male branch (left) and sporophyte; b, spores; c, germinated spore; d, axillary hair from perichaetium; e, epapillose cells of perichaetial bracts, side view and surface view; f, transverse section of perichaetial bract; g, transverse sections of upper parts of leaves; h, cells in upper part of leaf; i, cells of leaf base; j, juvenile leaves; k, mature leaves. (a, from Ben MacDhui, Jul 1856, herb. Meldrum, E; b, c, from Ben MacDhui, Aug 1854, _Croall, Plants of Braemar No. 72_, BM; d, from Riesengebirge, _Wihan_ in Musc. Eur. Am. Exs. 2002, NY; e, h, i, k [left], from Ben MacDhui, Jul 1835, _Croall_, BM; f, from Ben MacDhui, Jul 1873, _Fergusson_, E; g [two upper], from Transylvanian Alps, _Peterfi_ in Fl. Rom. Exs. 2604, B; g [lower], from Riesengebirge, Löwengraben, no date, _Kern s.n._, B; j, from Switzerland, Grimsel, no date, _Schimper s.n._, BM-Hooker)


b
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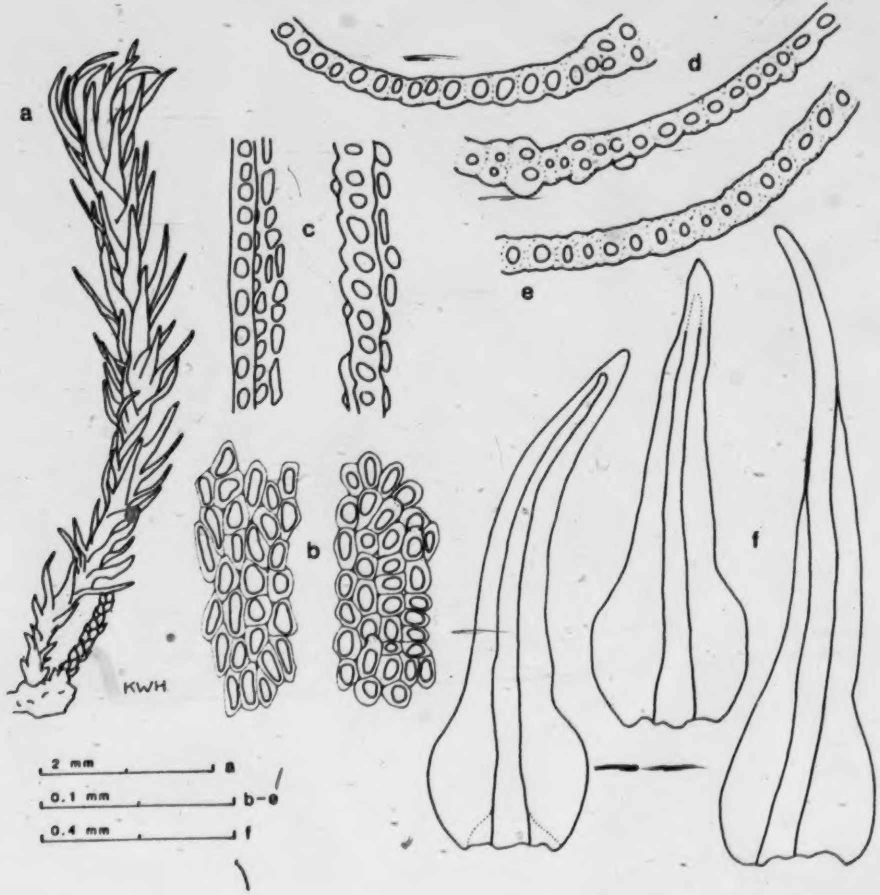
2 mm a
0.1 mm b–i
0.4 mm j,k

Figure VI-5. Illustrations of *Andreaea rothii* ssp. *rothii*: a, habit, sterile plant with juvenile shoot from protonema; b, surface views of cells of perichaetial bracts, epapillose (left) and with low, scattered papillae (right); c, side views of cells of perichaetial bracts, epapillose (left) and with low, scattered papillae (right); d, transverse sections of perichaetial bracts, epapillose (above) and with low, scattered papillae (below); e, transverse section of epapillose perichaetial bract with some joint thickenings; f, leaves. (a, e, f [right], from Haddington, Sep 1928, *J*. *B*. *Duncan*, ALA; b-d, from isotype of *A*. *rothii* var. *hamata*, Luggielaw, Jul 1873, *Lindberg*, NY; f [two left], Loch Maree, *Long 13850*, E)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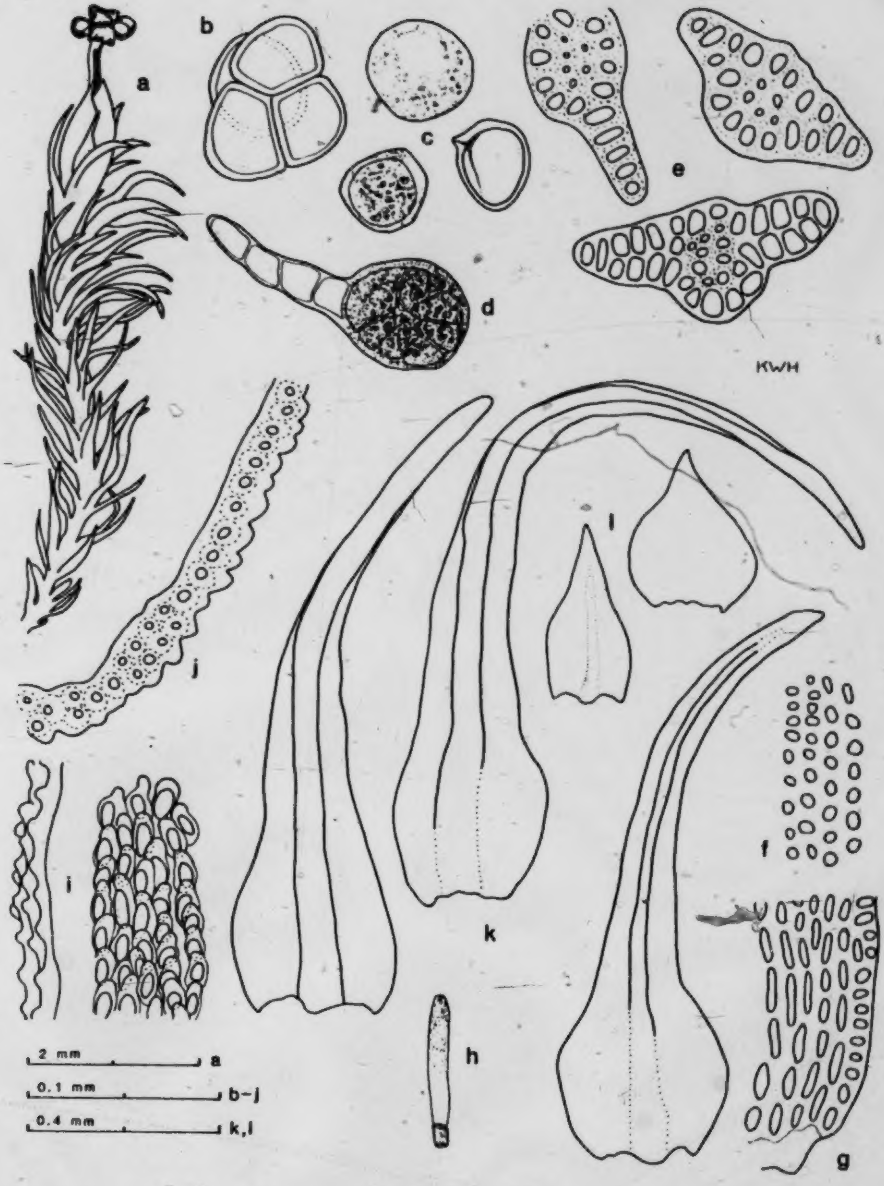
2 mm a
0.1 mm b-e
0.4 mm f

Figure VI-6. Illustrations of Andreaea rothii ssp. falcata: a, habit, plant with sporophyte; b, tetrad, from immature capsule, spores still hyaline; c, spores; d, germinated spore; e, transverse sections of upper part of leaves; f, cells in upper part of leaf; g, marginal cells of leaf base; h, axillary hair; i, papillose cells of perichaetial bracts, side view and surface view; j, transverse section of perichaetial bract; k, mature leaves; l, juvenile leaves. (a,d, l from Pass of Glencoe, 31 Jul 1984, Murray & Perry, ALA; b, from Glen Esk, Sep 1945, U. K. Duncan, E; c [upper], f, g, from Gleann Dubh, Jul 1978, Schofield, UBC B36259; c [two lower], e [lower], h, i, from Plynlimon, 12 Jul 1984, Murray & Perry, ALA; e [two upper], k, from Pass of Glencoe, 31 Oct 1982, Murray & Long, ALA; j, no data, from Wilson, Musc. Brit. 3, MO)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2 mm a
0.1 mm b–j
0.4 mm k, l

Figure VI-7. Illustrations of *Andreaea megistospora* ssp. *megistospora*: a, habit, female plant with perichaetium; b, habit (dry), plants with sporophytes; c, transverse sections of upper part of leaves; d, cells in upper part of leaf; e, marginal cells of leaf base; f, axillary hair; g, transverse section of perichaetial bract; h, germinated spore, i, brown spore, from immature capsule; j, papillose cells of perichaetial bracts, side view and surface view; k, transverse section of stem; l, juvenile leaves; m, mature leaves. (a, c-g, i-l, m [left], from holotype, Pass of Glencoe, 31 Oct 1982, *Murray & Long*, E; b, from British Columbia, *Schofield 24985*, UBC; h, from British Columbia, *Halbert 7594*, UBC; m [right] from Ben Nevis, 1 Aug 1984, *Murray & Perry*, ALA)

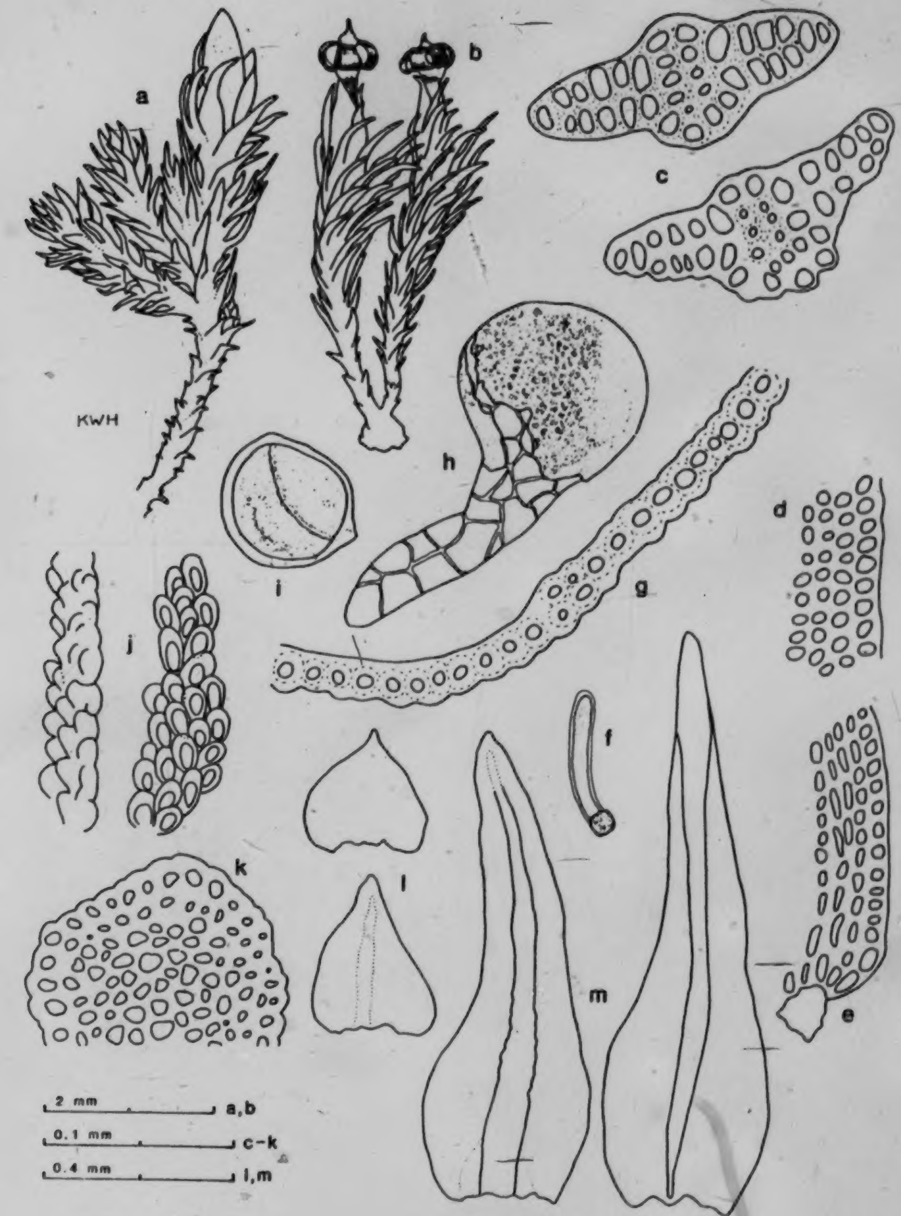
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Figure VI-8. Illustrations of *Andreaea alpina*: a, habit, plant with sporophyte; b, shrivelled and turgid spores; c, germinated spore; d, transverse sections of upper part of leaves, e, transverse section of leaf base; f, axillary hair; g, cells in upper part of leaf; h, marginal cells of leaf base; i, mature leaf with long attenuate apex; j, mature leaves; k, juvenile leaves. (a, from Beinn na h Uamha, *Schofield 69343*, UBC; b, from Ben Lawers, Jul 1808, *W. J. Hooker*, BM; c, from Plynlimon, 12 Jul 1984, *Murray & Perry*, ALA; d, g, h, j [left], from Meall nan Tarmachan, 30 Oct 1982, *Murray & Long*, ALA; e, j [right], from Meall nan Tarmachan, 15 Jul 1985, *Murray et al.*, ALA; i, from Cym Idwal, 26 Jun 1954, *Evans et al.*, S; k, from Caenlochan Glen, 14 Jul 1985, *Murray & Long*, ALA)

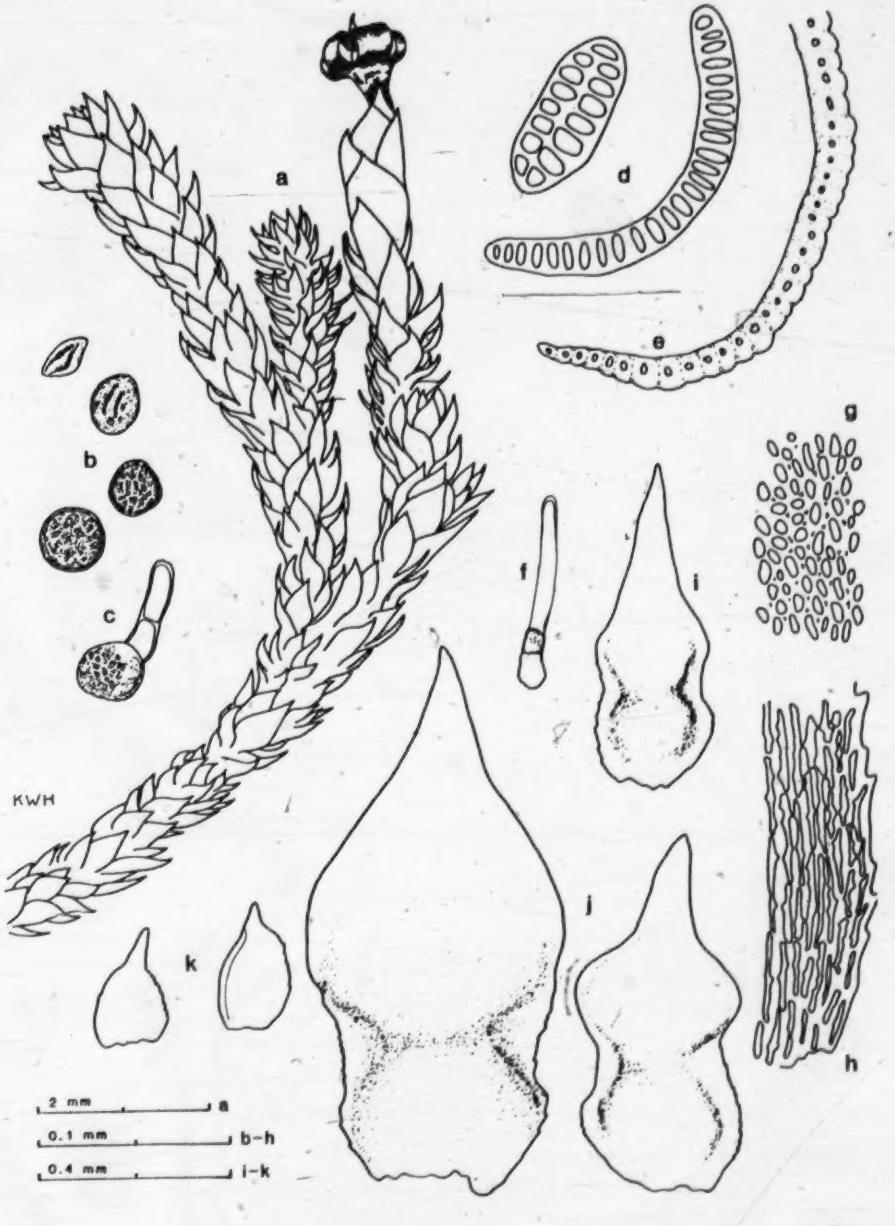
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Figure VI-9. Illustrations of Andreaea sinuosa: a, habits, left with sporophyte, right (dry), showing juvenile leaves; b, transverse section of stem; c, tetrad and spore; d, germinated spores; e, axillary hair; f, transverse sections of leaf base, showing joint thickenings; g, transverse sections of upper part of leaves; h, ventral view of cells in upper part of leaf; i, cells of leaf base and axillary hairs; j, mature leaves; k, juvenile leaves. (a-f, i-k from holotype, Canada, Schofield 74208, UBC; g, h, from Canada, Schofield 37892, ALA)

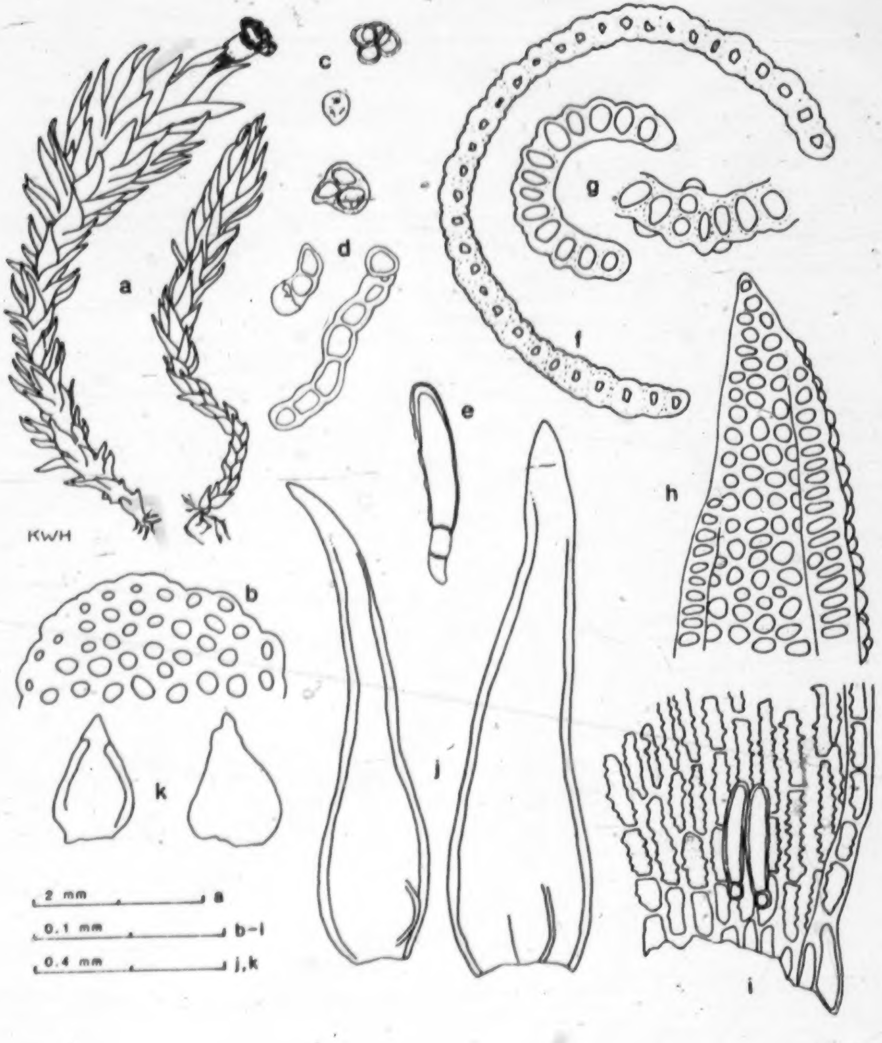
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Figure VI-10. Illustrations of *Andreaea mutabilis*: a, habit, male plant; b, habit, plant with sporophyte; c, ventral view of leaf base and insertion, with axillary hairs; d, transverse section of stem; e, tetrad and spore; f, germinated spore; g, transverse section of upper part of leaf; h, ventral view of cells in upper part of leaf; i, cells of leaf base, yellow area stippled; j, juvenile leaves; k, mature leaves. (a, d-f, h-j, k [left], from Ben Nevis, 1 Aug 1984, *Murray & Perry*, ALA; b, from Patagonia, *Skottsberg 107*, S; c, k [right], from Ben MacDhui, Jul 1909, *A. Wilson & Wheldon*, BM; g, from New Zealand, May 1889, *Beckett*, H)

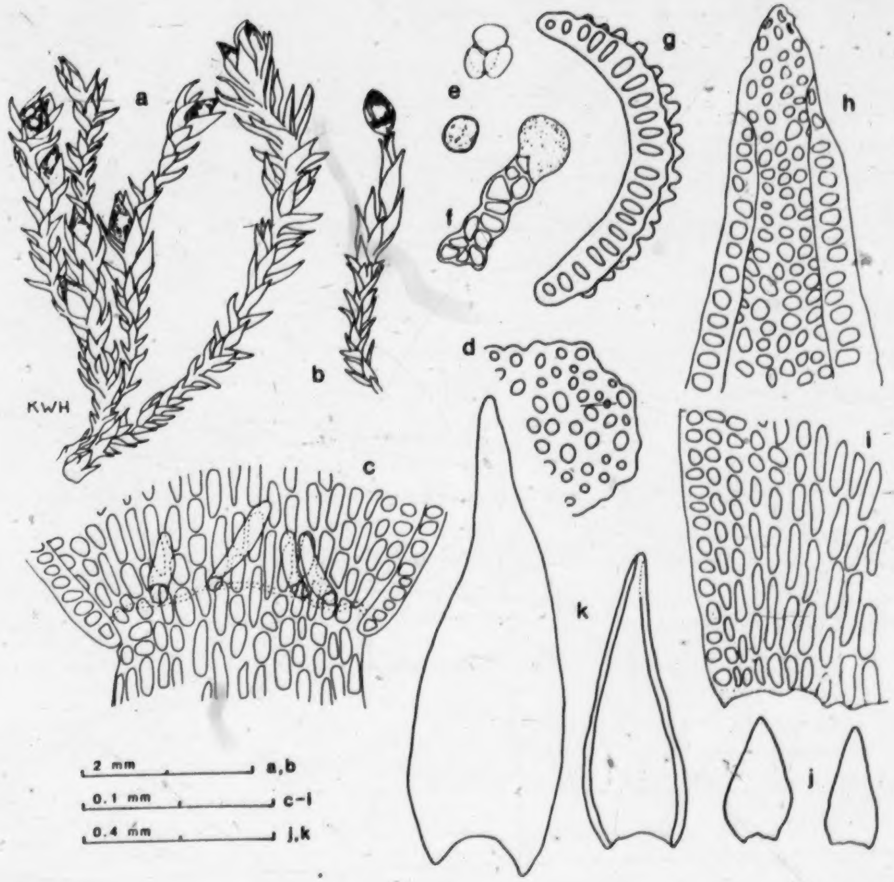
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Figure VI-11. Illustrations of *Andreaea rupestris*: a-h, i [upper] j,k, m-p, var. *rupestris*: a, habit, homomallous plant with sporophyte; b, tetrad from young, green capsule, spores tan and finely papillose; c, tetrad showing two aborted and two living spores; d, shrivelled aborted spore (above) and turgid living spore; e, germinated spore; f, transverse section of stem; g, axillary hair; h, transverse section of leaf base; i [upper], transverse section of upper part of leaf; j, cells in upper part of leaf; k, cells of leaf base; m, mature leaf, long acuminate form; n, mature leaf; o, panduriform mature leaf; p, juvenile leaves. i [lower], l, var. *papillosa*: i [lower] transverse section of upper part of leaf; l, mature leaf. (a, f, p, from Loch Lubnaig, 14 Apr 1970, *Henderson*, E; b, n, from Ben Nevis, 1 Aug 1984, *Murray & Perry*, ALA; c, g, o, from Pass of Glencoe, 31 Oct 1982, *Murray & Long*, ALA; d, e, j, k, m, from Cairn Gorm, 2 Aug 1984, *Murray & Perry*, ALA; h, i [lower], from near Carnedd Llewelyn, *Townsend 78/572*, herb. Townsend; i [upper], l, from near Dolgellau, 27 Jul 1964, *Townsend*, herb. Townsend)

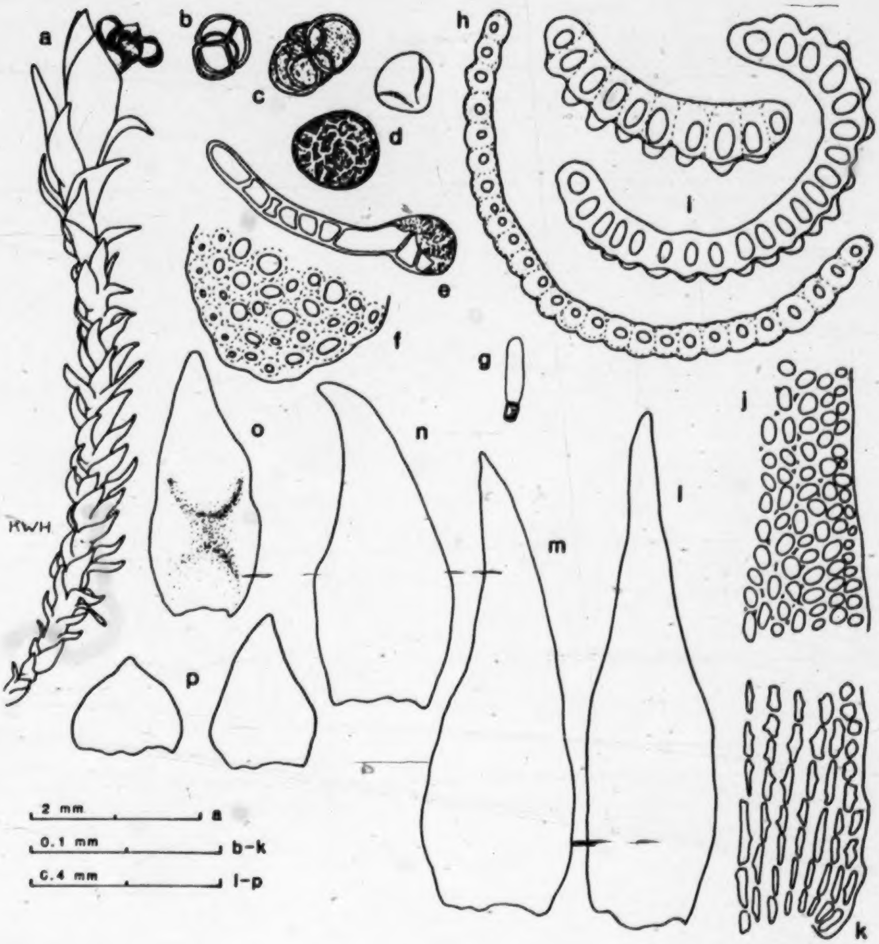
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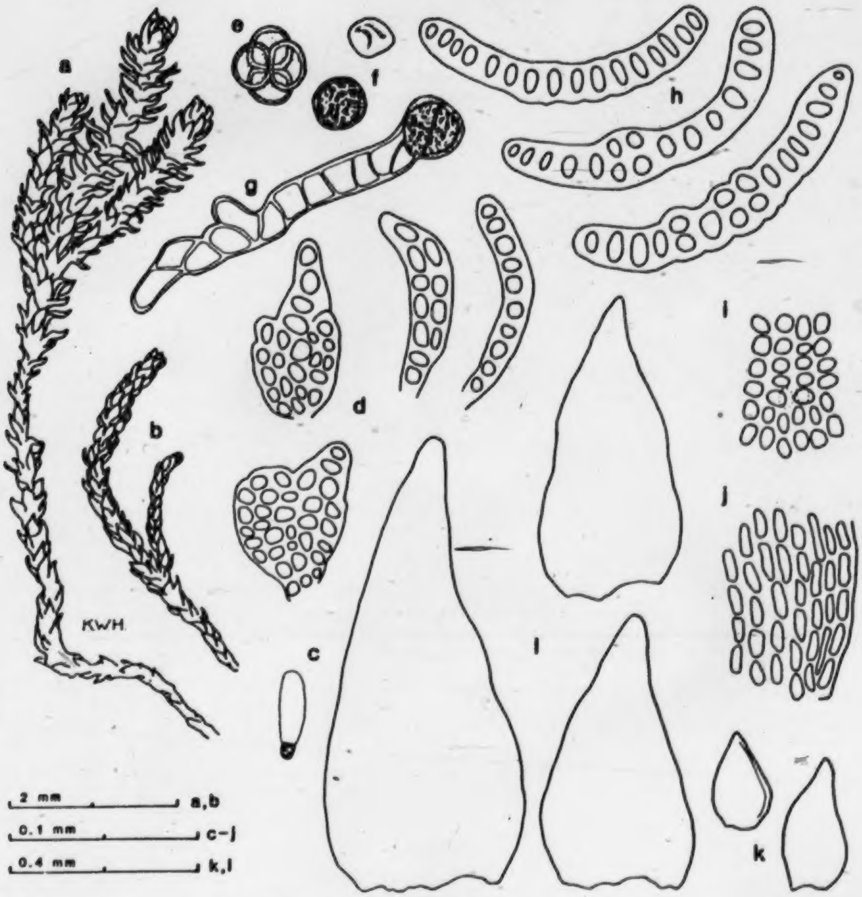
Figure VI-12. Illustrations of *Andreaea alpestris*: a, habit; b, habit (dry); c, axillary hair; d, primary leaves; e, tetrad, from young, green capsule, spores tan and finely papillose; f, shrivelled aborted spore (above) and turgid living spore; g, germinated spore; h, transverse sections of upper part of leaves; i, cells in upper part of leaf; j, cells of leaf base; k, juvenile leaves; l, mature leaves. (a, b, k, from Beinn a'Bhuird, 13 Jul 1985, *Murray & Long*, ALA; c, e, from Caenlochan Glen, 14 Jul 1985, *Murray & Long*, ALA; d, from Ben Nevis, *Long 13541*, E; f, g, from Ben Nevis, 1 Aug 1984, *Murray & Perry*, ALA; h, from Greenland, *Holmen & Mogensen 71-676*, C; i, j, l [two at right], from Cairn Gorm, 2 Aug 1984, *Murray & Perry*, ALA; l [left], from Alaska, *Steere 63-555*, ALA)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VII. GENERAL DISCUSSION AND CONCLUSIONS

The long-standing systematic difficulties and perplexities of the Andreaeopsida have resulted from several factors. First is the great systematic isolation of the group from other bryophytes. In addition, lack of a sufficient fossil record and huge gaps in morphological markers place inferences as to relationships on a shaky, perhaps even groundless foundation. Given these constraints (which apply to bryophyte systematics generally), it has been possible, nevertheless, to propose a new taxonomic framework for the Andreaeopsida, since the group has been analyzed in some detail for the first time.

The primary circumstance that has led to the taxonomic proposals and revamped classification presented here is the use of new characters. I have treated Andreaeobryum and Andreaea, the two included genera in the Andreaeopsida, as representing two separate orders because of the fundamental morphological differences between them. These differences, tabulated in Chapter II (Table II-1), include features seen in Andreaeobryum that are not known in other mosses: the cylindric shape of the photosynthetic protonemal appendages; beaked mucilage papillae; the occurrence of mucilage papillae on both protonemata and gametophores; and a perichaetium that consists of compressed spirals of numerous, variable bracts, develops after fertilization, and encloses only the fertilized archegonium. The corresponding features in Andreaea are similar to those in other mosses. Anomalous features of Andreaeobryum find their closest counterparts only in the even more systematically mysterious taxon, Takakia. It seems likely to me, based on the morphological evidence presented here, that mosses and hepatics (at least the lines represented by the Andreaeopsida, Takakiopsida, and Haplomitriopsida) have common ancestry and that the ancestor of bryophytes had features that have been retained in the patristically primitive *Andreaeobryum* and *Takakia*. It will be interesting to see if features such as beaked mucilage papillae can be found in the fossil record of early land plants and if further study of the problem will permit the hypotheses presented here to stand.

Just as the discovery of new characters caused a re-evaluation of the taxa in higher categories and of the phylogenetic placement of the Andreaeopsida, similar use of new characters has led to the recognition of new taxa and to a realignment of other taxa within the genus *Andreaea*.

For example, within subg. *Andreaea* the traditional circumscription by presence or absence of a costa for sections *Nerviae* Card. *ex* Broth. and *Andreaea* should be re-examined. Several ecostate species, *A. sinuosa* B. Murr. and *A. alpina* Hedw. for example, share features with costate taxa. It may be that the presently constituted sections are not natural and when the entire genus has been studied systematic rearrangement should be proposed.

The main difference between the present treatment of North American and European *Andreaeae* and prior work is the result of my selection of spore size as a major taxonomic criterion. For example, *Andreaea sinuosa* and *A. mutabilis* Hook. f. & Wils. have small spores, which help to separate the species decisively from the *A. rupestris* group (including *A. rupestris* Hedw., *A. alpestris* (Thed.) Schimp., and *A. obovata* Thed.) with its medium-sized spores. But it is in sect. *Nerviae* that I have proposed a systematic arrangement that is an almost complete reversal of the one recently put forward (Schultze-Motel 1970). Conventional treatment of costate *Andreaeae* in subg. *Andreaea* has been the alliance of taxa on the basis of leaf characters. I have not stressed these characters, since I found that their expressions vary and recur throughout the genus *Andreaea*. In contrast, spore size is a constant and reliable marker. This analysis is presented in tabular form in Chapters IV and VI (Tables IV-1, VI-3).

As a result of the emphasis on spore size and de-emphasis of the costa-lamina relationship in leaves, taxa previously referable to or treated as *A. rothii* web. & Mohr (Schultze-Motel 1970)--*A. rothii* ssp. *rothii*, *A. schofieldiana* B. Murr., *A. frigida* Hüb., and *A. megistospora* B. Murr. ssp. *megistospora*--are here treated as separate species representing medium, large and very large spore size classes. Taxa previously referable to or treated as *A. crassinervia* Bruch (Schultze-Motel 1970)--*A. crassinervia*, *A. rothii* ssp. *falcata* (Schimp.) Lindb. (= *A. crassinervia* ssp. *huntii* [Limpr.] Amann), and *A. megistospora* ssp. *epapillosa* B. Murr.--are here treated as separate species that also represent medium, large, and very large spore size classes. Further, these latter taxa (with *crassinervia*-type leaves, sensu Schultze-Motel 1970) are systematically closely related to their counterparts in spore size in the group with *rothii*-type leaves (sensu Schultze-Motel 1970).

As a result of study of about 10,000 herbarium specimens I have concluded that the North American (north of Mexico) and European *Andreaea* flora consists of 14 species, four subspecies, and two varieties: *A. nivalis* Hook., *A. blyttii* Schimp., *A. heinemannii* Hampe & C. Müll., *A. crassinervia*, *A. frigida*, *A. schofieldiana*, *A. rothii* ssp.

rothii, *A*. *rothii* ssp. *falcata*, *A*. *megistospora* ssp. *megistospora*, *A*. *megistospora* ssp. *epapillosa*, *A*. *alpina*, *A*. *sinuosa*, *A*. *mutabilis*, *A*. *rupestris* var. *rupestris*, *A*. *rupestris* var. *papillosa* (Lindb.) Podp., *A*. *alpestris*, and *A*. *obovata*. All but *A*. *frigida* (a European endemic) and *A*. *schofieldiana* and *A*. *megistospora* ssp. *epapillosa* (known only from northwestern North America) occur in both North America (including Greenland) and Europe. This listing contrasts with the most recent checklists for North America and Europe. For North America (excluding Greenland) Crum et al. (1973) listed six species and two varieties; for Europe Corley et al. (1981) listed eight species.

A pressing need in bryophyte systematics is a worldwide revision of the genus *Andreaea* (see also Scott 1982). Based on my background study of *Andreaea* taxa worldwide, I anticipate the approach that has proved useful for Northern Hemisphere taxa will also help in revising the seemingly intractable but incompletely studied *Andreaeae* in the Southern Hemisphere.

Several problems in *Andreaea* systematics seem to have no hope of solution until experimental propagation and transplant studies are performed. The polymorphic *A*. *rupestris* and its close allies, *A*. *alpestris* and *A*. *obovata*, remain as puzzling to me now as they were before I had examined several thousand specimens. Traditional herbarium methods are inadequate to deal with the perplexing, overlapping variation of the group. Similar problems are rampant in Southern Hemisphere taxa, centering around *A*. *acutifolia* Hook. f. & Wils. and its allies.

I am continuing monographic study of the group, and I hope that the compilation of the state of knowledge of systematics of the

Andreaeopsida presented here will draw attention to the many gaps that remain and will stimulate further study of the group, especially experimental propagation and chemical, cytological, ultrastructural, and morphogenetic analyses.

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